PATTERNS IN FUNCTIONAL STRUCTURE AND DIVERSITY OF STREAM FISH ASSEMBLAGES RELATED TO ENVIRONMENTAL FACTORS AT MULTIPLE SCALES

A Dissertation

by

ALLISON ANN PEASE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2010

Major Subject: Wildlife and Fisheries Sciences

Patterns in Functional Structure and Diversity of Stream Fish Assemblages Related to Environmental Factors at Multiple Scales

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Approved by:

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ABSTRACT

Patterns in Functional Structure and Diversity of Stream Fish Assemblages Related to Environmental Factors at Multiple Scales. (December 2010)

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Chair of Advisory Committee: Dr. Kirk O. Winemiller

The distribution and abundance of stream fishes are influenced by many factors operating at multiple scales. Understanding how environmental variables influence the structure of stream fish assemblages is important for habitat assessment, stream restoration, and for predicting responses to environmental change. An emerging view in community ecology is that a focus on the functional structure of species assemblages in relation to environmental gradients may reveal more general patterns applicable across geographic regions. In this study, I used functional traits related to the trophic ecology, habitat use, and life-history strategies of fishes to examine the influences of environmental factors on stream fish assemblages. The research was carried out in two large regions: the Río Grijalva basin in southern Mexico and the Brazos and Trinity basins in Central Texas. In both regions, relationships between functional structure of stream fish assemblages and environmental factors at local, landscape, and regional scales were examined.

Environmental characteristics at all three scales influenced the functional attributes of assemblages studied here. At the local reach scale, stream size, substrate characteristics, the availability of riffle and pool habitats, and abundance of in-stream cover structures were related to the functional trait composition of fish assemblages in the Río Grijalva Basin and in Central Texas streams. Landscape features most strongly related to functional structure in both regions were the extent of forested area in the watershed and the amount of land developed for urban and agricultural uses. At the

regional scale, broad physiographic differences between ecoregions had a large influence on the taxonomic and functional composition of stream fish assemblages in Central Texas. Along the broad-scale longitudinal fluvial gradient of the Grijalva region, pronounced changes in the species composition, functional trait diversity, and trophic structure of fish assemblages were observed.

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TABLE OF CONTENTS

Page

ABSTRACT iii

ACKNOWLEDGEMENTS v

TABLE OF CONTENTS vii

LIST OF FIGURES ix

LIST OF TABLES xi

CHAPTER

I INTRODUCTION: FUNCTIONAL STRUCTURE OF STREAM FISH ASSEMBLAGES ALONG ENVIRONMENTAL GRADIENTS 1

II FISH ASSEMBLAGE STRUCTURE AND FUNCTIONALTRAIT DIVERSITY ALONG ENVIRONMENTAL GRADIENTS IN A TROPICAL RIVER BASIN, THE RIO GRÍJALVA, MEXICO 4

- Introduction 4
- Methods 7
- Results 17
- Discussion 26

III CHANGES IN TROPHIC STRUCTURE OF STREAM FISH ASSEMBLAGES ALONG THE LONGITUDINAL FLUVIAL GRADIENT OF THE RIO GRIJALVA, MEXICO 31

- Introduction 31
- Methods 32
- Results 36
- Discussion 42

CHAPTER Page

IV FUNCTIONAL TRAIT DIVERSITY AND TRAIT-ENVIRONMENT RELATIONSHIPS IN CENTRAL TEXAS STREAM FISH ASSEMBLAGES: IMPLICATIONS FOR BIOMONITORING 46

Introduction 46
Methods 49
Results 59
Discussion 68

V CONCLUSIONS 73

LITERATURE CITED 75

VITA 84

LIST OF FIGURES

FIGURE		Page
1	Map of the study region, the Río Grijalva watershed, in Chiapas and Tabasco, Mexico	8
2	NMS ordination of Río Grijalva stream reaches based on species composition of fish assemblages.	19
3	PCA ordination of Río Grijalva stream reaches based on local and landscape-scale environmental variables	20
4	PCA ordination of Río Grijalva fish species in two dimensions of functional trait-space	22
5	Position of Río Grijalva species in functional trait-space	23
6	Ordination of RLQ scores of environmental variables and functional traits of Río Grijalva fish species	25
7	Regression of species richness and three indices of functional diversity on latitude for the Río Grijalva basin	26
8	Average volumetric proportions of eight broad trophic resource categories for assemblages in the Upper, Middle, and Lower Grijalva regions	37
9	PCA ordination of Río Grijalva species based on proportional volume of prey items in stomach contents	38
10	Regression of dietary niche overlap and volume of trophic space occupation of Río Grijalva fish assemblages on latitude	40
11	NMS ordination of Río Grijalva stream reaches based on trophic group composition of fish assemblages	41
12	NMS ordination of Río Grijalva fish assemblages showing the abundance of trophic groups	42
13	Map of study region in the Brazos and Trinity Basins of Texas	49
14	NMS ordination of Central Texas stream reaches based on species composition of local fish assemblages	60

FIGURE Page

15 PCA ordination of Central Texas stream reaches based on local and landscape-scale environmental variables 62

16 PCA ordination of Central Texas fish species in two dimensions of functional trait-space 64

17 Ordination of RLQ scores of environmental variables and functional traits of fish species for Central Texas stream reaches 66

18 Regressions of convex hull volumes of functional trait occupation of Central Texas fish assemblages against species richness, IBI and HQI scores, and scores from the primary environmental axis 68

LIST OF TABLES

TABLE		Page
1	Local and landscape-scale environmental variables recorded for Río Grijalva study sites	10
2	List of the 27 functional traits used for Río Grijalva fish assemblages with measurement methodology	13
3	Trophic group assignments and regional affiliations of Río Grijalva species captured in this study	35
4	Local-scale environmental variables (57) measured at Central Texas stream reaches	52
5	Landscape-scale environmental variables estimated for Central Texas streams	54
6	List of the 29 functional traits used for Central Texas fish assemblages with measurement methodology	55
7	Results of the RLQ analyses for Central Texas stream fish assemblages	65

CHAPTER I

INTRODUCTION: FUNCTIONAL STRUCTURE OF STREAM FISH ASSEMBLAGES ALONG ENVIRONMENTAL GRADIENTS

A fundamental question for ecologists studying stream fish assemblages is: what determines which fishes occur where? Many studies have been conducted to address this question, and the answer is complicated. The distribution and abundance of stream fishes are influenced by many factors operating at multiple scales (Schlosser 1987, Poff 1997, Marsh-Matthews and Matthews 2000). An understanding of the environmental influences on stream fish assemblages is necessary for habitat assessment, stream restoration, and for predicting how assemblages will respond to environmental change. Here I sought to clarify the relationships between the functional structure of stream fish assemblages and environmental variables in two large regions: the Río Grijalva basin in southern Mexico and the Brazos and Trinity basins in Central Texas. I examined environmental influences at three spatial scales: local reach (in-stream habitat conditions), landscape (characteristics of the surrounding watershed), and regional scale (position along longitudinal fluvial gradient).

Though many studies have documented relationships between environmental variables and the presence or abundance of particular fish species in streams, few general relationships that apply across geographic regions have been documented. Incorporating a functional rather than taxonomic approach may reveal more broadly applicable relationships (Poff and Allan 1995, Angermeier and Winston 1999, Hoeinghaus et al. 2007). A focus on functional traits as they relate to environmental gradients can reveal more general patterns and improve our ability to predict responses of natural communities to environmental change (McGill et al. 2006, Poff et al. 2006, 2006, Olden et al. 2010). In the studies outlined here, I used functional traits related to

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This dissertation follows the style of Ecology.

the trophic ecology, habitat use, and life-history strategies of fishes to examine the influences of environmental factors on fish assemblages in a more mechanistic manner (Chapters II and IV). For the study described in Chapter III, I focused on patterns of trophic structure of fish assemblages along a broad fluvial gradient.

Ecologists have long recognized that ecosystem processes and biological community structure change along fluvial gradients within river basins (e.g., Hynes 1970, Horwitz 1978, Vannote et al. 1980). Patterns of discharge, availability of production sources, and species interactions differ along with abiotic environmental characteristics that transition from headwaters to downstream reaches. The functional structure of aquatic communities also is expected to change along the course of a river basin from upstream tributaries to lowland streams (Vannote et al. 1980, Schlosser 1987).

In Chapters II and III, I examine these changes along the fluvial gradient of the Río Grijalva in southern Mexico. When it joins the Río Usumacinta in Tabasco, it is the largest river in Mesoamerica, yet little is known about the ecology of the fishes in this region. Hence, part of the motivation for the research outlined in these chapters was to document the distribution and basic ecology of fishes in streams of the Grijalva basin. In Chapter II, I examine the influence of environmental variables on the functional traits of stream fish assemblages from the highlands to the lowlands along the fluvial gradient of the Río Grijalva Basin. I conducted this study in 20 streams across a range of environments within the Grijalva watershed. The broad spatial extent of the study region allowed me to examine environmental influences at local and landscape scales across a range of habitat types. In Chapter III, I explicitly examine the trophic structure of fish assemblages in the same stream sites. My objective with this study was to determine how the abundance of trophic guilds, diversity of food resource use, and dietary niche overlap within local fish assemblages change along the Río Grijalva fluvial gradient.

In the study described in Chapter IV, I used a functional-traits approach (as in Chapter II) to identify relationships between at local and landscape-scale environmental

variables and the functional structure of 64 stream fish assemblages in a large region of Central Texas. In addition, I examined how the functional diversity of these assemblages relates to established measures of habitat quality and biotic integrity. Documenting trait-environment relationships may provide valuable information for determining the potential use of functional traits of fish assemblages as a means of monitoring the environmental quality of streams.

The three chapters outlined above focus on patterns in functional structure of stream assemblages in relation to local, landscape, and regional environmental factors. The incorporation of a functional approach should make the results of these studies applicable to research on fish assemblages in other rivers across geographic regions. In Chapter V, I summarize the findings of the previous chapters and highlight areas requiring further investigation.

CHAPTER II

FISH ASSEMBLAGE STRUCTURE AND FUNCTIONAL TRAIT DIVERSITY ALONG ENVIRONMENTAL GRADIENTS IN A TROPICAL RIVER BASIN, THE RIO GRÍJALVA, MEXICO

Introduction

The distribution and abundance of stream fishes are influenced by many factors operating at multiple scales (Schlosser 1987, Poff 1997). Understanding how environmental variables influence the structure of stream fish communities is important for habitat assessment, stream restoration, and for predicting how assemblages will respond to environmental change. Local-scale habitat variables, such as substrate composition, pool dimensions, and the amount of available cover have been shown to correlate strongly with fish assemblage structure (e.g., Ibarra and Stewart 1989, Fischer and Paukert 2008, Rowe et al. 2009a). Many local environmental characteristics are shaped by larger-scale features in a drainage basin such as underlying geology, riparian vegetation, and fluvial geomorphology (Frissell et al. 1986, Richards et al. 1996), and the role of landscape-level factors in shaping stream communities is increasingly recognized (Allan 2004). In order to examine the influences of local and landscape-scale environmental variables on stream fish communities, studies at broad spatial scales are needed.

Across watersheds of large rivers, stream environments generally change in predictable ways. Stream size, hydrological variability, diversity of habitat types, and availability of in-stream production sources are some key environmental variables that shift along the fluvial gradient from upland headwaters to downstream reaches (Hynes 1970, Horwitz 1978, Vannote et al. 1980). The River Continuum Concept (RCC, Vannote et al. 1980) provides a framework for predicting how aquatic communities change along with longitudinal abiotic changes in large river basins. According to the RCC, changes in food availability along the fluvial continuum constrain the trophic groups of aquatic organisms within communities. Based on this concept, fish species

that are generalized invertebrate feeders are expected in upstream reaches, while omnivores, detritivores, herbivores and piscivores become more abundant in streams further downstream in a river basin (Vannote et al. 1980, Schlosser 1987). Recently, Thorp et al. (2008) outlined the Riverine Ecosystem Synthesis which incorporates previous work on hierarchical patch dynamics and describes river networks as arrays of hydrogeomorphic patches ("functional process zones") instead of longitudinal continua as described in the RCC. Temporal variability and habitat complexity of these patches influence functional community structure, and patches within longitudinal zones of a basin may be no more similar than those upstream or downstream (Poole 2002).

Townsend and Hildrew's (1994) River Habitat Template (RHT) theory also makes predictions about how stream communities change across large-scale gradients. The RHT predicts that two main features, temporal variability and spatial heterogeneity, influence the traits of species in stream communities. In streams with high temporal variability and low spatial heterogeneity (e.g., flashy headwater streams), the RHT predicts that species are more likely to have traits that confer resistance and resilience such as small body size, streamlined shape, high fecundity, and short reproductive cycles. Temporally stable streams with a variety of habitats for refugia from disturbance are expected to support species with a more diverse range of traits. Poff (1997) proposed the idea of "landscape filters," which describes how environmental variables select for traits of species from the watershed to the microhabitat scale. For example, at the watershed scale, seasonality of flow may constrain the life-history strategies of species. Progressively finer filters at the stream reach and microhabitat scales, such as riparian conditions and substrate composition, may influence the trophic and reproductive guilds present in a local species assemblage.

An emerging view in community ecology is that a focus on functional traits as they relate to environmental gradients can reveal general patterns and improve our ability to predict responses of natural communities to environmental change (McGill et al. 2006, Poff et al. 2006, Olden et al. 2010). The theoretical frameworks above allow for explicit predictions of how functional traits of fishes respond to environmental

factors at multiple scales. Testing these concepts for stream fish assemblages across large fluvial gradients has been difficult, however, due to limited knowledge of functional traits, and most previous studies have examined the relationships across gradients in relatively small watersheds. A large-scale study by Lamouroux et al. (2002) examined the relationships between reach-scale stream hydraulics and geomorphology and six functional traits related to swimming, habitat use and life history for fish assemblages in France and Virginia. They found that in both continents, these environmental variables were related to traits such as body shape, fecundity, and habitat preference within stream communities. Other broad-scale studies have generally assigned fish species to functional groups or guilds rather than examining specific functional traits. For example, Poff and Allan (1995) found that hydrologically variable streams were more likely to contain generalists in terms of trophic guild and substrate preference. Similarly, Ibañez et al. (2009) found that the proportion of invertebrate feeders decreased while the proportion of omnivores increased from upstream to downstream reaches in streams in four continents.

In large tropical rivers, few studies have examined changes in fish assemblage structure at the watershed scale, and little is known about how the functional structure of species assemblages responds to environmental change in these systems. The goal of this research was to examine the influence of environmental variables on the functional traits of stream fish assemblages from the highlands to the lowlands along the fluvial gradient of the Río Grijalva Basin of southern Mexico. The broad spatial extent of the study region allowed me to examine environmental influences at local and landscape scales across a range of habitat types. The incorporation of a functional-traits approach provided a more mechanistic framework for us to examine the influences of environmental factors on fish assemblages. Specifically, my objectives were to examine changes in assemblage structure along the fluvial gradient of the Río Grijalva basin and to identify relationships between functional traits of species and environmental variables at multiple scales within the region.

Methods

Study region description

The Río Grijalva begins in Guatemala and flows through the states of Chiapas and Tabasco in southern Mexico. As the Grijalva nears the Gulf of Mexico in Tabasco, it joins the Río Usumacinta, and together they form the largest river in Mesoamerica. Approximately 115 species from 31 families have been documented in the region, and an estimated 36% of species are endemic (Miller 2005). This study focuses on wadeable streams within the Grijalva basin above its confluence with the Río Usumacinta, an approximately 60,000-km^2 region (Figure 1). The environmental characteristics of stream habitats within the Grijalva basin change markedly along a longitudinal gradient from the mountainous Sierra Madre de Chiapas to the coastal plains in Tabasco. Upland, high-gradient streams in the headwaters give way to broad and sinuous channels in the middle sections, and ultimately the channels are transformed into a mosaic of wetlands before draining into the Gulf of Mexico (Hudson et al. 2005). Upland stream habitats are more environmentally harsh, with high temporal variation in flow, less spatial heterogeneity and fewer low-velocity microhabitats in local communities. Further downstream on the fluvial gradient, stream habitats become progressively more stable, with more low-velocity pools, more structurally complex microhabitats, and a broader prey resource base. We designated the area above the Angostura reservoir as the "Upper Grijalva," the portion of the watershed below Angostura and above the Malpaso reservoir as the "Middle Grijalva," and the section below Malpaso to the confluence with the Río Usumacinta as the "Lower Grijalva."

I conducted this study in 20 streams across a range of environments within the Grijalva watershed. The study sites were selected to ensure roughly equal representation in upper, middle, and lower portions of the basin with data from a range of stream orders (from small headwaters to broad, high-order, major tributaries).

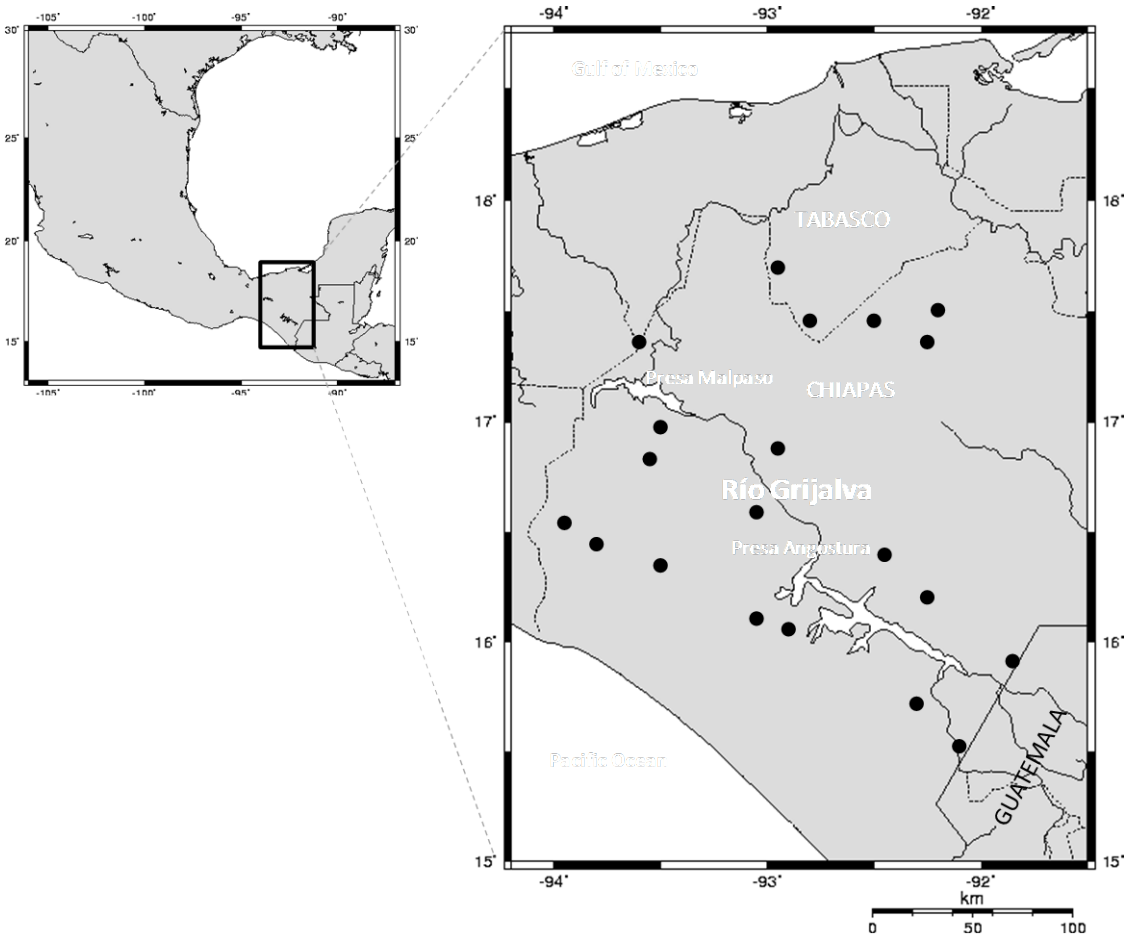

Figure 1. Map of the study region, the Río Grijalva watershed, in Chiapas and Tabasco, Mexico. Solid dots indicate locations of surveyed stream reaches.

I sampled the 20 streams during March and April of 2008 and 2009. These months are within the dry season for this region, a time when flows are lower and fish can be captured more efficiently. At each survey site, a 200-m stream reach encompassing all available macrohabitat types (e.g., pools, runs, and riffles) was designated for fish collection and local habitat measurements. Within each study reach, fishes were collected by performing a minimum of six seine hauls of 10 m (seine dimensions = 5 x 2 m, 5-mm mesh). Where appropriate, sampling was supplemented using a cast net (2-m diameter, 1-cm mesh). In sites with rocky substrate where seining was inefficient, fishes were sampled using a backpack electrofisher (Smith-Root Model

LR-24). Electrofishing was performed with a single pass moving upstream across the entire study reach. Collected fishes were identified, counted, and either released into the habitat or preserved in 10% buffered formalin for later identification. Preserved fishes were deposited in the museum collection of El Colegio de la Frontera Sur in San Cristobal de las Casas, Chiapas.

At each study site, 34 local habitat variables were measured (Table 1). Prior to fish sampling, water temperature (°C), dissolved oxygen (mg/L), specific conductivity (μS), and salinity were measured using a handheld meter (YSI model 85). Average wetted width, average depth, and thalweg depth were calculated based on measurements taken across three transects within the study reach. Water velocity (m/s) was measured at 60% depth at ten evenly spaced points across each transect using a portable electromagnetic flow meter (Marsh-McBirney Flo-Mate Model 2000). Depth and water velocity measurements were used to calculate a velocity-depth regime score reflecting the diversity of flow and depth habitats available within the study reach. The score is based on the number of different velocity-depth regimes present following the methods of U.S. Environmental Protection Agency stream bioassessment protocols (Plafkin et al. 1989). Canopy cover was measured using a spherical densiometer at four locations across each transect in order to calculate the average percent cover. To characterize substrate composition, the percentage of bedrock, large boulders (>45 cm diameter), small boulders (26-45 cm), cobble (6-25 cm), gravel (2-60 mm), sand (0.06-2 mm), and mud/silt (<0.06 mm) were visually estimated. I also estimated the proportion of in-stream structural cover provided by rocks, large and small woody debris, roots, leaf packs, aquatic vegetation, overhanging terrestrial vegetation, algae, undercut banks, and artificial structures. The overall average percent of stream habitat containing structural cover was estimated visually for each reach. The number of riffles within the study reach, maximum pool depth, and maximum pool width also were recorded. I scored the abundance of algae and aquatic macrophytes within the reaches as abundant, common, rare, or absent. The width of the riparian buffer on each bank was estimated in meters.

Following the method of Plafkin et al. (1989), an aesthetics score was assigned to each study site based on the extent of local habitat alteration.

Topographic maps, publicly available databases, and field observations were used to compile eight additional environmental variables at the landscape or regional scale (Table 1). I measured geographic position (latitude and longitude in decimal degrees) using a handheld GPS unit at the time of in-stream and riparian habitat data collection. Elevation, stream order and distance to the main stem of the Rio Grijalva were measured using 1:250,000 scale topographic maps available from the Mexican federal agency for geography and statistics (Instituto Nacional de Estadística y Geografía, INEGI). Annual precipitation data were obtained from Mexican federal databases (Comisión Nacional de Agua, http://smn.cna.gob.mx). Percent forest cover within the watershed was estimated from digital maps of land cover also obtained from INEGI. Population density in the surrounding watershed was estimated from maps produced by the United Nations Food and Agriculture Organization.

Table 1. Local and landscape-scale environmental variables recorded for Río Grijalva study sites.

Category	**Abbreviation**	**Variable**
Substrate	BEDROCK	Percent of substrate - bedrock
	LG_BLDR	Percent of substrate - large boulders (>45 cm)
	SM_BLDR	Percent of substrate - small boulders (25-45 cm)
	COBBLE	Percent of substrate - cobble (6-25 cm)
	GRAVEL	Percent of substrate - gravel (2-60 mm)
	SAND	Percent of substrate - sand (0.06-2 mm)
	MUDSILT	Percent of substrate - mud or silt (<0.06 mm)
	GRV_LRG	Percent of substrate - gravel or larger
Algae/ macrophytes	ALGAE_AB	Abundance of algae in study reach (scored as abundant, common, rare, or absent)
	MCRPH_AB	Abundance of aquatic macrophytes in study reach (scored as abundant, common, rare, or absent)

Table 1. Continued.

Category	Abbreviation	Variable
In-stream cover	STRM_COV	Visually estimated percent cover
	FILA_ALG	Percent of cover - filamentous algae
	MACRPHYT	Percent of cover - aquatic macrophytes
	LWD	Percent of cover - large woody debris
	SWD	Percent of cover - small woody debris
	ROOTS	Percent of cover - submerged roots
	OVR_VEG	Percent of cover - overhanging terrestrial vegetation
	UNDERCUT	Percent of cover - undercut banks
	LEAFPACK	Percent of cover - submerged leaf packs
	BOULDER	Percent of cover - boulders and other large substrates
Stream morphology	WETWIDTH	Wetted width of stream (averaged across transects)
	THAL_DEP	Thalweg depth (averaged across transects)
	NO_RIFF	Number of riffles in study reach
	POOL_WID	Maximum pool width
	POOL_DEP	Maximum pool depth
	VELDEPTH	Velocity/depth regime score (optimal, suboptimal, marginal, or poor)
Local riparian buffer	BUFFER	Width of riparian buffer (averaged across transects)
	CANOPY	Percent of stream shaded by tree canopy (measured with densitometer)
	AESTHET	Aesthetics score (wilderness, natural area, common setting, or offensive)
Water parameters	DO	Instantaneous dissolved oxygen (mg/L)
	PH	pH
	SPCOND	Specific conductivity (μs)
	SALINITY	Salinity (ppt)
	TEMP	Water temperature (°C)
Landscape-scale variables	ELEV	Elevation (m)
	LAT	Latitude (decimal degrees)
	LON	Longitude (decimal degrees)
	PRECIP	Annual precipitation in watershed (mm)
	STRM_ORD	Stream order
	MAIN_DIS	Distance to main stem of Río Grijalva (km)
	FOREST	Percent forested land in watershed
	POP_DEN	Mean population density in watershed (people per km^2)

Functional traits

I measured 28 functional traits (Table 2) of at least three adult individuals of each fish species from each of the 20 stream survey sites. These traits were chosen because they have well known relationships with feeding, habitat use, swimming behavior, or life history strategies of stream fishes. For example, traits such as gape size, mouth position, head length and gut length relate to food resource use in fishes (Gatz 1979). Morphological features related to habitat preference and locomotion include relative body depth, fin dimensions, and dimensions of the caudal peduncle (Gatz, 1979, Webb 1984). I measured egg diameter and mean clutch size to reflect interspecific differences in life history strategies (Winemiller and Rose 1992). Traits were defined and measured following the methods of Winemiller (1991) for morphological traits and Winemiller and Rose (1992) for life history traits. For species with sexual dimorphism in these traits (e.g., the anal fin of poeciliids), only females were measured. All length measurements were made to the nearest 0.1 mm using vernier calipers. Because functional traits sometimes are not informative for community-level analyses if there is substantial within-species variation in trait values (McGill et al. 2006), I confirmed that interspecific variation was significantly greater than intraspecific variation by performing an F-test on the variance ($P < 0.05$) of all traits before carrying out multivariate analyses.

Table 2. List of the 27 functional traits used for Río Grijalva fish assemblages with measurement methodology. Trait definitions and functional categories follow Gatz 1979, Webb 1984, Winemiller 1991, Winemiller and Rose 1992, and Sibbing and Nagelkerke 2001.

Trait	**Trait code**	**Trait definition**	**Functional category**
Maximum standard length	MAX_SL	Maximum standard length from the populations in this study and published records	Habitat use, feeding, life history strategy
Head length	HEAD_L	Distance from the tip of the jaw to the posterior edge of the operculum	Feeding
Head depth	HEAD_D	Vertical distance from dorsum to ventrum passing through the pupil	Feeding
Oral gape	GAPE	Vertical distance measured inside of fully open mouth at tallest point	Feeding
Mouth position	MOUTH_P	The angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the center of the pupil and the posterior-most vertebra (e.g., 90° representing a terminal mouth)	Feeding, habitat use
Eye position	EYE_POS	Vertical distance from the center of the pupil to the ventrum	Habitat use
Eye diameter	EYE_D	Horizontal distance from eye margin to eye margin	Feeding
Snout length	SNT_L	Distance from the pupil to the tip of the upper jaw with mouth shut	Feeding
Snout protrusion	SNT_PR	Additional distance from the pupil to the tip of the upper jaw with mouth fully open and extended	Feeding
Body depth	BOD_D	Maximum vertical distance from dorsum to ventrum	Locomotion, habitat use
Body width	BOD_W	Maximum horizontal distance from side to side	Locomotion
Caudal peduncle length	PED_L	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra	Locomotion
Caudal peduncle depth	PED_D	Minimum vertical distance from dorsum to ventrum of caudal peduncle	Locomotion

Table 2. Continued.

Trait	Trait code	Trait definition	Functional category
Caudal peduncle depth	PED_D	Minimum vertical distance from dorsum to ventrum of caudal peduncle	Locomotion
Caudal peduncle width	PED_W	Horizontal width of the caudal peduncle at midlength	Locomotion
Body depth below midline	DEP_MID	Vertical distance from midline to ventrum*	Locomotion, habitat use
Dorsal fin length	DORS_L	Distance from the anterior proximal margin to the posterior proximal margin of the dorsal fin	Locomotion
Dorsal fin height	DORS_HT	Maximum distance from the proximal to distal margin of the dorsal fin (excluding filaments)	Locomotion
Anal fin length	ANAL_L	Distance from the anterior proximal margin to the posterior proximal margin of the anal fin	Locomotion
Anal fin height	ANAL_HT	Maximum distance from proximal to distal margin of the anal fin	Locomotion
Caudal fin depth	CAUD_D	Maximum vertical distance across the fully spread caudal fin	Locomotion
Caudal fin length	CAUD_L	Maximum distance from proximal to distal margin of the caudal fin (excluding filaments)	Locomotion
Pectoral fin length	PEC_L	Maximum distance from proximal to distal margin of pectoral fin	Locomotion, habitat use
Pelvic fin length	PELV_L	Maximum distance from the proximal to distal margin of the pelvic fin	Locomotion, habitat use
Gut length	GUT_L	Length of gut from the beginning of the esophagus to the anus (extended without stretching)	Feeding
Gill raker length	RAKER_L	Length of the longest gill raker	Feeding
Egg diameter	EGG_D	Mean diameter of mature (fully yolked) oocytes	Life history strategy
Clutch size	CLUTCH	Average clutch size (from published accounts for some species)	Life history strategy

Statistical analyses

I quantified among-site differences in taxonomic assemblage structure by performing non-metric multidimensional scaling (NMS) on log-transformed species abundances. Because it avoids assumptions of linearity, NMS is considered well suited for analyzing patterns in assemblage structure without some of the problems associated with other commonly used methods (McCune and Grace 2002). I used Bray-Curtis dissimilarity (BCD) as the distance measure, and retained a three-dimensional solution as stress values were substantially greater when only two axes were included in the ordination. A principal component analysis (PCA) was performed on log-transformed environmental variables (local and landscape-scale) to identify the primary environmental gradients among stream sites.

To examine among species differences in functional traits, a PCA was performed on the matrix of species traits. Because body size has a substantial influence on trait values, all traits were regressed against standard length and residuals were used as the trait values for the PCA. Mouth position, egg diameter, and clutch size were not correlated with body size so log-transformed values for these variables were used instead of residuals. The PCA was performed using the mean transformed values for each functional trait for each species. The NMS and PCA analyses were carried out using PC-ORD software version 5.2 (MjM Software, Gleneden Beach, OR, U.S.A.).

An RLQ analysis was used to relate patterns of environmental differences and functional traits of fish assemblages among sites. RLQ is a multivariate technique based on ordinations of three separate matrices (species abundance, environmental variables, and species traits). RLQ was proposed by Doledec et al. (1996) as an extension of co-inertia analysis to relate species traits directly to environmental characteristics through ordination of the matrix of species abundance for sites. The first step in RLQ analysis was the separate ordination of the species abundance, environmental variables, and species traits matrices. The “R” matrix containing the log-transformed environmental variables for the study sites was analyzed with PCA. The “L” matrix contains the log-transformed species abundances for sites, and correspondence analysis (CA) was used to

identify gradients in taxonomic assemblage structure following the RLQ specifications. Next, the functional traits of species in the "Q" matrix were analyzed using PCA on trait residuals. The significance of the relationship between the environmental variables (R) and functional traits of species (Q) was tested with a Monte Carlo permutation test with 1000 random permutations of the rows of both the functional traits and environmental variables matrices (Doledec et al. 1996). The ADE-4 package (Dray and Dufour 2007) for R version 2.10.1 (The R Foundation for Statistical Computing) was used for all analyses associated with the RLQ.

Trait diversity was calculated for each fish assemblage using three multidimensional functional diversity indices that reflect functional trait-space occupation, functional evenness and functional divergence as described by Villeger et al. (2008). The multivariate volume of trait space occupied by each local fish assemblage was measured using the convex hull volume method of Cornwell et al. (2006). Because trait dimensions cannot be greater than the number of species when calculating the convex hull volume for local assemblages, I used the scores for the first six PC axes from the functional traits PCA for species' traits. These calculations were performed with the Quickhull algorithm (Barber et al. 1996) in MATLAB software (Mathworks Inc., 2009). Functional evenness, which describes the evenness of the distribution of species in functional trait space, was calculated following Villeger et al. (2008). Functional divergence, which describes how abundance is distributed in relation to the center of gravity of the functional trait space of a community, was calculated using the FDiv equation of Villeger et al. (2008). The FD package (Laliberte and Legendre 2010) for R version 2.10.1 (The R Foundation for Statistical Computing) was used to calculate functional evenness and divergence.

Results

Species composition

A total of 33 species were collected from the streams sampled in our study region. Local stream fish assemblages were dominated by the Cichlidae and Poeciliidae, the two families that dominate the freshwater ichthyofauna of Mesoamerica overall. Non-native tilapia (*Oreochromis* species, family Cichlidae) were present at five sites in the Middle Grijalva region. Species richness ranged from 1 in the high-elevation Río Lajas to 14 in one Middle Grijalva stream and one Lower Grijalva stream. Species richness increased with latitude, with generally more species present in communities further downstream along the general south-north fluvial gradient of the Grijalva basin. A few species were collected throughout the basin (e.g., *Astyanax aeneus*, *Rhamdia guatemalensis*); however patterns of species turnover from uplands to lowlands due to longitudinal zonation in species distributions were apparent. Four cichlid species, *Vieja hartwegi*, *Cichlasoma grammodes, Amphilophus macracanthus*, and *Cichlasoma trimaculatum* were found only in streams within the Upper and Middle Grijalva region. Further downstream in the basin, these were replaced by lowland cichlids such as *Cichlasoma salvini*, *Chuco intermedium*, *Vieja bifasciata*, and *Thorichthys species*. Among poeciliids, *Poecilia sphenops* and *Poeciliopsis* species were abundant in communities in the Upper and Middle reaches, whereas a more diverse suite of species including *Poecilia mexicana*, *Heterandria bimaculata, Belonesox belizanus*, *Xiphophorus hellerii* and *Priapella* species were collected in lowland streams. Two killifish species, *Profundulus labialis* and *Profundulus punctatus*, were collected only in higher elevation streams in the Middle and Upper Grijalva.

The NMS analysis identified three axes that explained 89.5% of the variance in abundance of species among sites (Figure 2). Sites appear to separate on the first axis (37.5% of variance) according to elevation and position along the fluvial gradient. Sites plotting on the left side of axis 1 had the lowest species richness and contained highland species such as *Vieja hartwegi*, *Cichlasoma grammodes*, and *Profundulus* species. Local fish assemblages plotting on the right side of the first axis were more species rich

and contained lowland species such as *Atherinella alvarezi*, *Poecilia mexicana*, and *Thorichthys* species. The second axis (33.4% of variance) appeared to separate Middle Grijalva sites dominated by sand substrate (high scores on axis 2) from sites in the Upper and Lower regions with rocky substrate (low scores on axis 2). Species assemblages that plotted high on axis 2 contained *Cichlasoma salvini and Poecilipsis fasciata*. Species preferring habitats with coarse substrate such as *Theraps lentiginosus* were more abundant in stream reaches with low scores on axis 2. The third axis (18.6% of variance) revealed a gradient that contrasted dryer regions that had higher abundances of *Profundulus labialis*, *Amphilophus macracanthus*, and *Poeciliopsis fasciata* to wetter zones characterized by species such as *Chuco intermedium* and *Xiphophorus hellerii*.

Environmental variables

The first three axes of the PCA of environmental variables explained 48.1% of variation among sites (Figure 3). The dominant gradient (PC1, 23.6% of variance) was most strongly associated with substrate type, depth, and the diversity of flow-depth regimes. Sites with high scores on axis 1 had sandy substrates and relatively shallow channels with few pool habitats. These sites were mostly within the Middle Grijalva region, but included some streams in the Upper and Lower sections. Sites with low scores on axis 1 had rocky substrates, more diverse mesohabitats, and deeper channels. Most Lower Grijalva streams had negative scores on axis 1. The second gradient (PC2, 12.8% of variance) revealed a gradient that contrasted sites having more forest cover in the landscape, wider riparian buffers, more riffle habitats, and more in-stream cover from wood and leaves with sites having less forest cover, wider channels, and more aquatic macrophytes. The third axis (11.7% of variance) contrasted sites on the basis of elevation, latitude, precipitation, distance to the Grijalva main stem, human population density, and algal abundance.

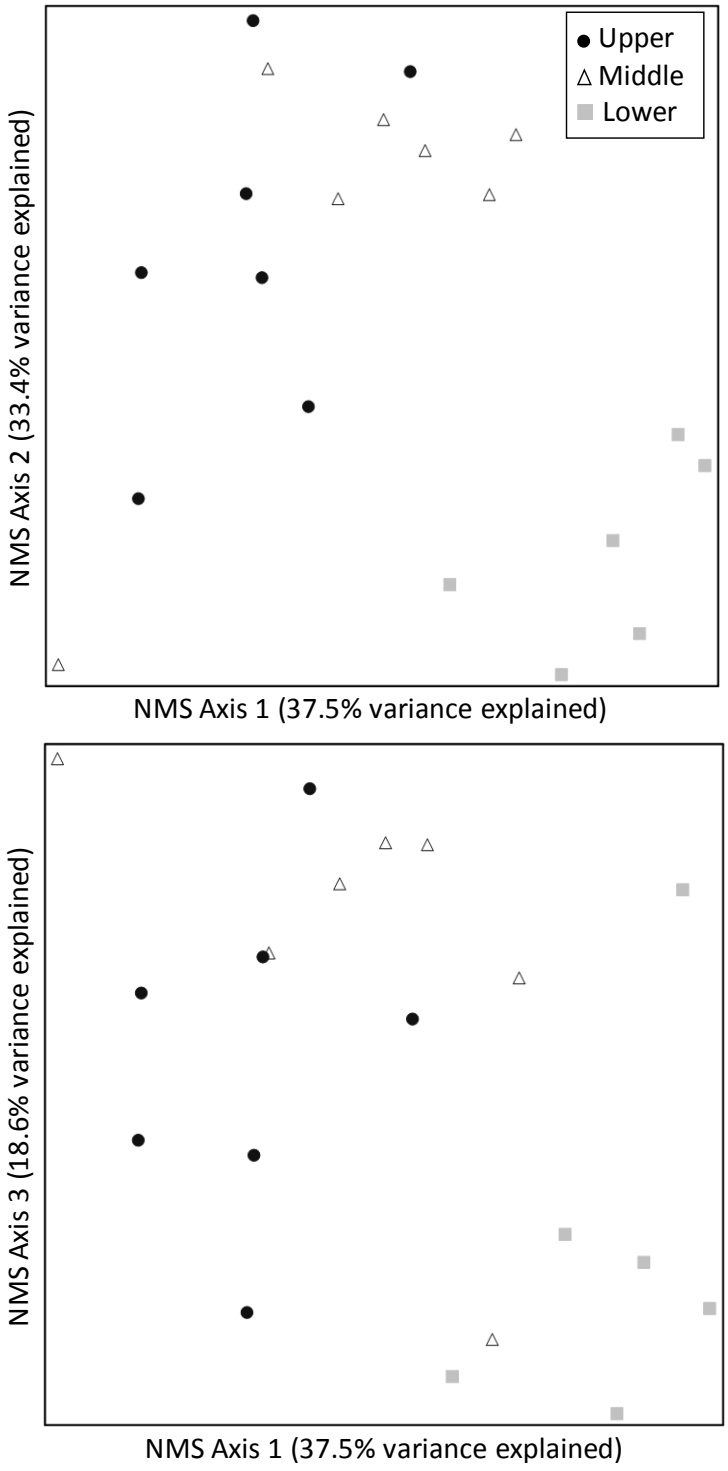

Figure 2. NMS ordination of Río Grijalva stream reaches based on species composition of fish assemblages.

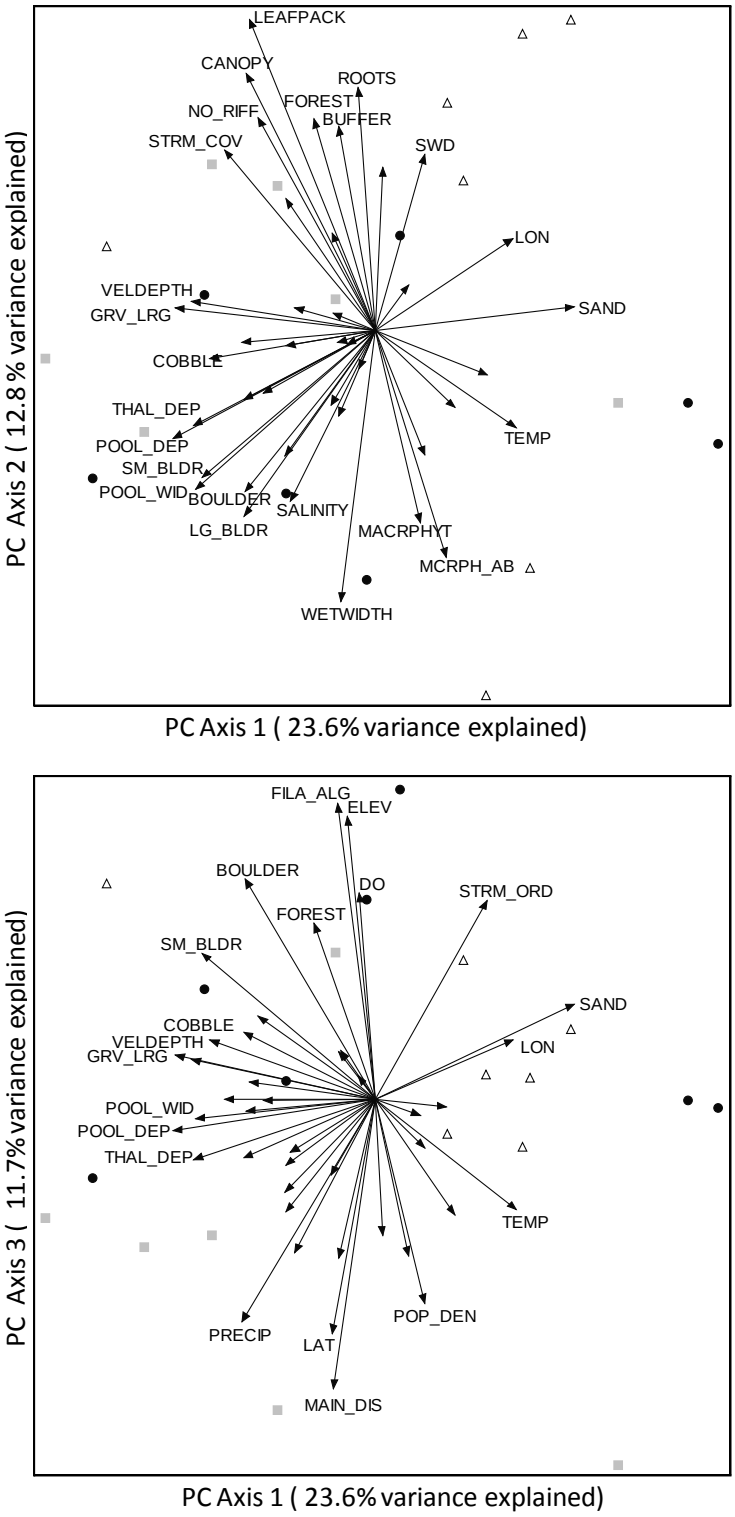

Figure 3. PCA ordination of Río Grijalva stream reaches based on local and landscape-scale environmental variables.

Trait-environment relationships

PCA performed on functional traits resulted in two axes that explained 66.3% of variance among species (Figure 4). The primary axis (PC1, 49.2% of variance) largely reflected differences in head length and depth, body depth, fin lengths, and eye diameter. Cichlid species with relatively large heads and snouts, long fins, and deep bodies had low scores on axis 1 (Figure 5). Catfishes (*Rhamdia* spp.) and killifishes (*Profundulus* spp.) have relatively streamlined bodies, short fins and small eyes, and had high scores on axis 1. Axis 2 (17.1% of variance) contrasted species with different life history strategies (e.g., egg diameter, clutch size) as well as differences in gill raker length, mouth position, and maximum body size. The two characid species have large clutch sizes, small eggs, and relatively longer gill rakers, and these species had high scores on axis 2. Poeciliid species, which have relatively small clutches of large eggs, small body sizes and upturned mouths, had low scores on axis 2. Axis 3 (8.8% of variance) reflected a gradient of trophic traits (e.g., differences in gape size, snout protrusion, and gut length). Species with relatively long snouts, larger gapes, and relatively short gut lengths had high scores on axis 3. These species, including *Belonesox belizanus*, *Cichlasoma grammodes* and *Theraps lentiginosus*, tend to feed on macroinvertebrates or other fishes. Herbivorous fishes, such as *Oreochromis aureus* and *Poecilia* species, have very long intestines and had the lowest scores on axis 3.

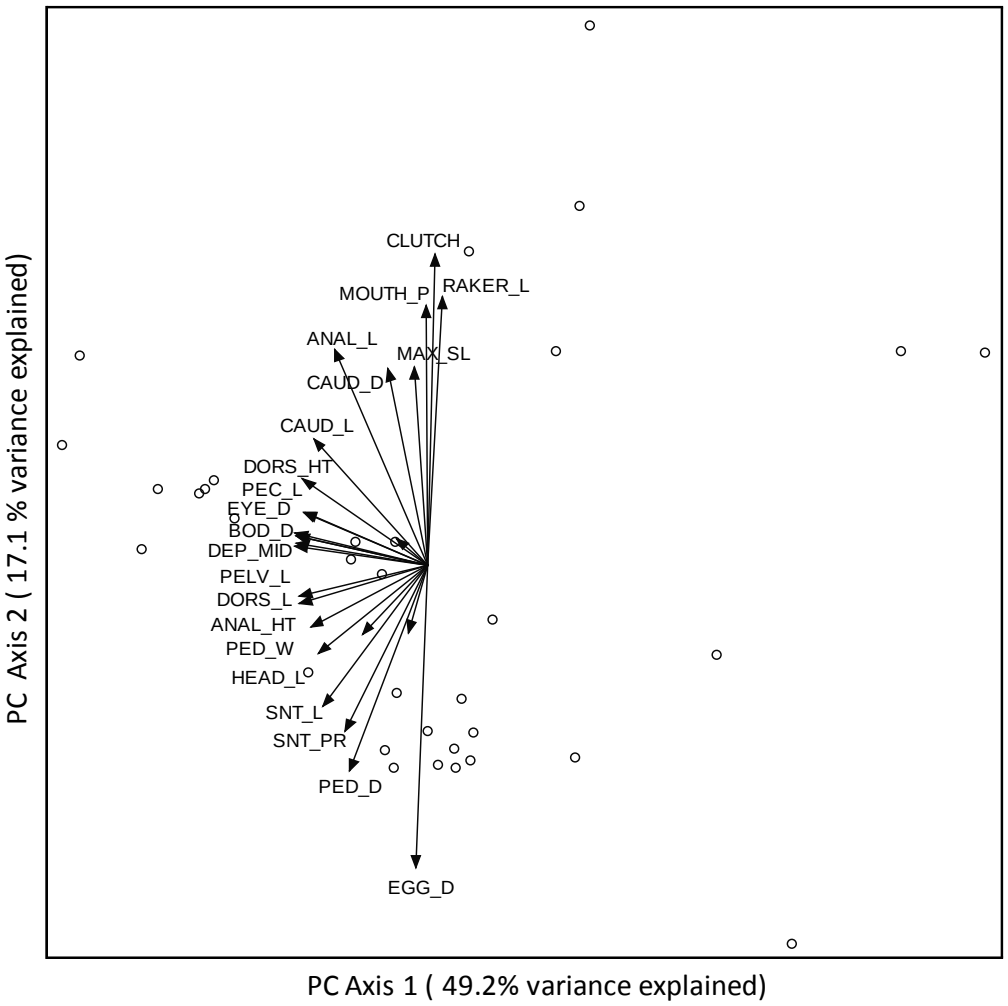

Figure 4. PCA ordination of Río Grijalva fish species (open circles) in two dimensions of functional trait-space. Trait loadings on the two axes are depicted as vectors.

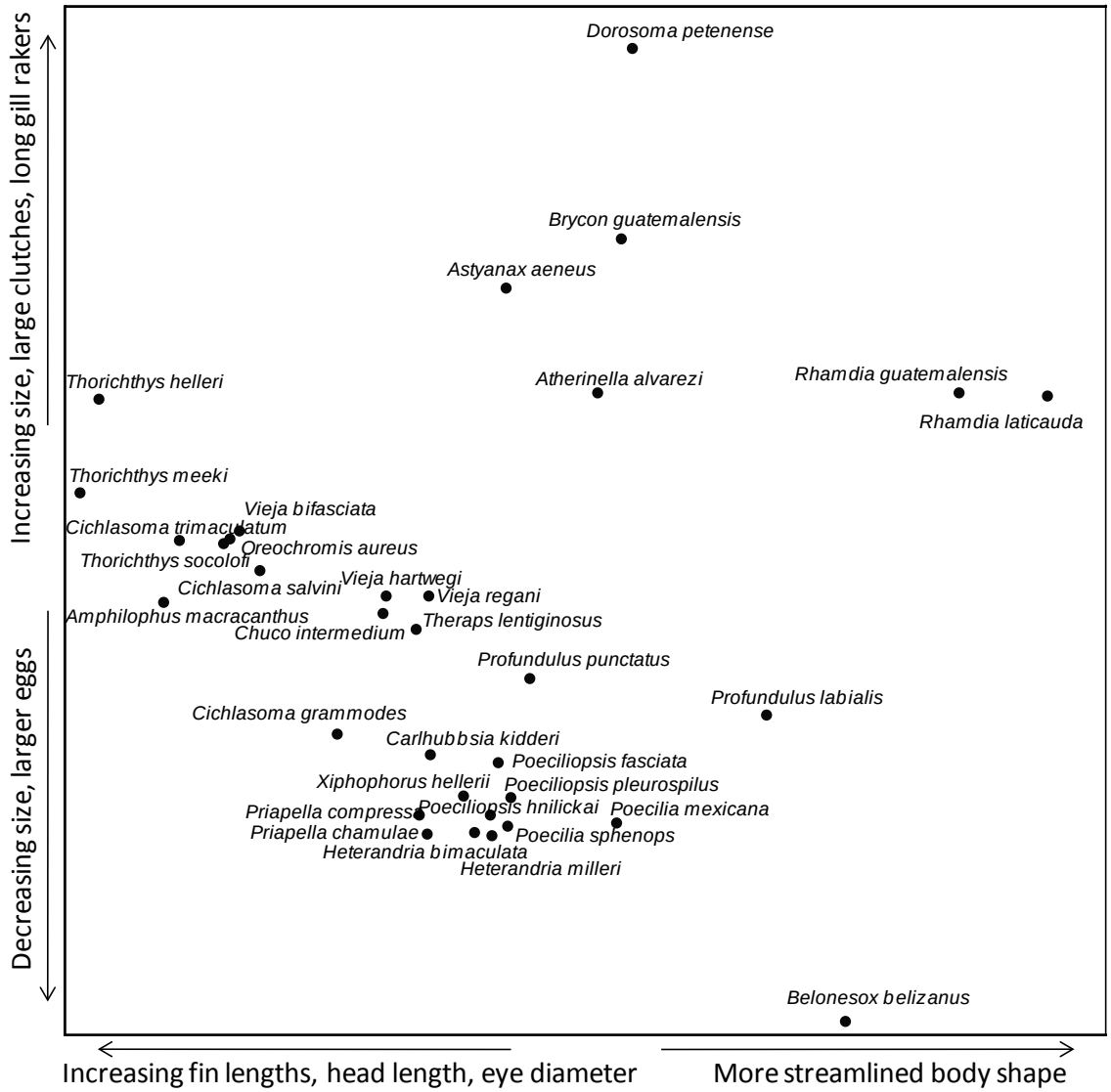

Figure 5. Position of Río Grijalva species in functional trait-space (2-dimensional PCA ordination from Fig.4).

The first two axes of the RLQ accounted for 33.8% and 19.3%, respectively, of the total variance in the matrix that related the environmental characteristics of sites to the functional traits of species. The permutation test showed that the relationship between functional traits and environmental variables was greater than expected at

random given the regional species pool, but the relationship was not considered statistically significant (P = 0.09, 1000 permutations). The first RLQ axis corresponded with changes in latitude, elevation, and climate corresponding with the longitudinal fluvial gradient of the Grijalva (Figure 6). Environmental variables with highly positive correlations with the first axis included elevation, percent sand in substrate, and longitude. Annual precipitation, latitude, pool and channel depth, and proportion of rocky substrate had high correlations with RLQ axis 1 on the negative side. Gape and body width of species were functional traits positively associated with the high elevation, sandy streams on axis 1. Traits plotted on the opposite end of axis 1 (lower on the fluvial gradient with wetter climates, deeper habitats, and rocky substrate) included larger eye diameter, deeper body, and longer head, snout and fins. Sites with more riffle habitats, abundant in-stream cover, and a higher percentage of forest cover in the landscape were positively associated with RLQ axis 2. Traits correlated with RLQ axis 2 include gill raker length, egg diameter, and mouth position (higher scores on RLQ axis 2 were associated with more inferior mouth positions). Environmental variables associated negatively with RLQ axis 2 included stream width, aquatic macrophyte abundance, pH and temperature. Functional traits that correlated with these variables on axis 2 included gut length, caudal peduncle width, body depth below the midline, body width, and clutch size.

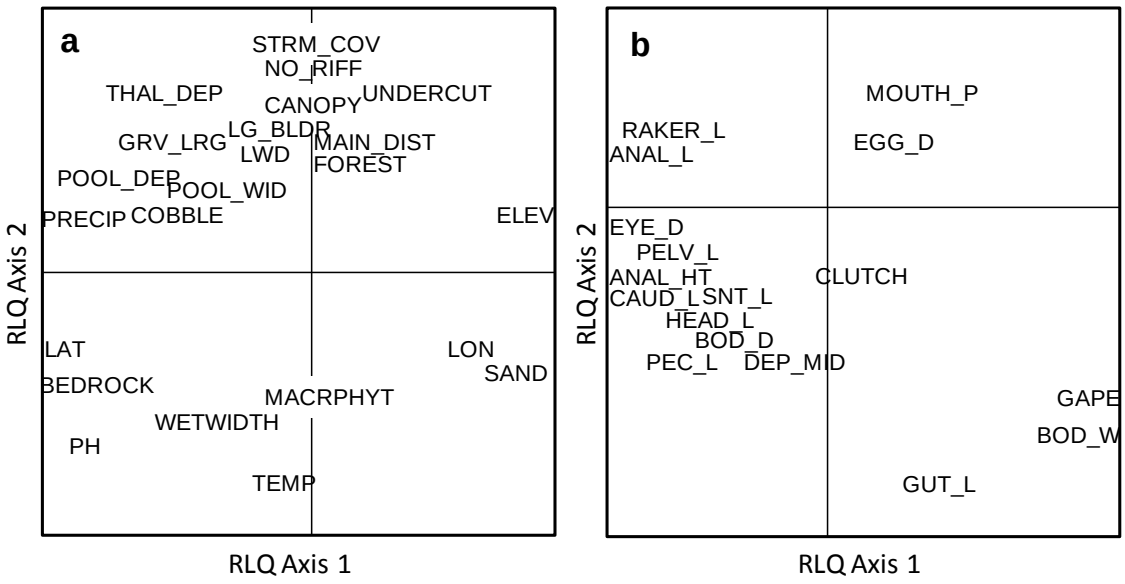

Figure 6. Ordination of RLQ scores of environmental variables and functional traits of Río Grijalva fish species. See tables 1 and 2 for environmental variables and functional traits that correspond to abbreviations.

Functional diversity along the fluvial gradient

The volume of functional trait space occupied by fish assemblages generally increased along with species richness from the highlands in the south to the lowlands in the north on the fluvial gradient of the Grijalva Basin (Figure 7). Sites with the largest convex hull volumes of functional trait space as well as highest species richness were in the Lower Grijalva region. Streams with similarly high species richness in the Middle Grijalva had lower functional richness, indicating that faunal shifts in the region affected the functional space occupied by fish assemblages. The Lower Grijalva streams that had the fewest species also had disproportionately lower functional diversity. These sites lacked certain lowland species, such as *Belonesox belizanus* and *Thorichthys helleri*, which are morphologically distinctive. Functional evenness, a measure of regularity and spacing between species in functional trait space, was generally higher in more species-rich streams positioned lower in the fluvial gradient. Several streams with low species richness in the highlands also had high functional evenness despite having a lower range

of trait values (smaller volume in trait space). There was no relationship between functional divergence and elevation. Hence, the degree of average species divergence from the center of trait space did not increase in species-rich lowland assemblages, even though total functional trait diversity was greater.

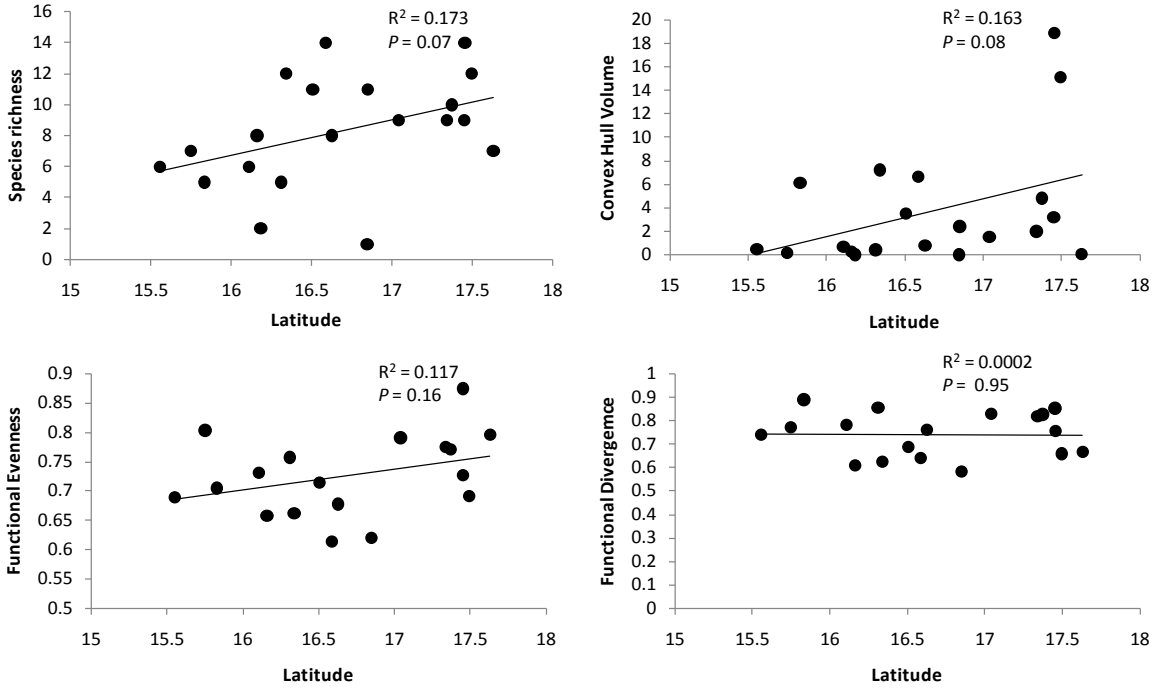

Figure 7. Regression of species richness and three indices of functional diversity on latitude for the Río Grijalva basin. Latitude corresponds to a great extent with the fluvial gradient of the Río Grijalva, which flows from south to north.

Discussion

As shown for other large watersheds, stream fish assemblages within the Río Grijalva Basin displayed patterns of longitudinal zonation in structure. Faunal turnover was apparent as we examined fish assemblages from the highlands in southern Chiapas to the more mesic lowlands of the Grijalva Basin. Ordination of stream sites based on

species composition revealed that differences in species assemblage structure corresponded with the position of streams along the fluvial gradient. In general, species richness increased with latitude and decreasing elevation along the fluvial gradient. These findings are consistent with patterns observed for fish assemblages in rivers and streams globally. Zonation in distribution of fishes along the fluvial gradient of large river basins in other regions has been related to differences in climate, geology, disturbance frequency, stream hydraulics, and habitat size that correspond with fluvial position in the watershed (e.g., Horwitz 1978, Ibarra and Stewart 1989, Hoeinghaus et al. 2004, Esselman et al. 2006). In the Grijalva basin, faunal zonation seems to follow regional gradients in climate, elevation, stream size, and substrate composition. Species richness has been shown to increase from upstream to downstream along river gradients in both temperate and tropical regions (e.g., Horwitz 1978, Rahel and Hubert 1991, Osborne and Wiley 1992, Edds 1993, Gerson Araujo et al. 2009). Streams located further downstream are expected to support more diverse fish assemblages as they become larger, warmer, more hydrologically stable, and more spatially heterogeneous (Schlosser 1987).

In this study, I found that a variety of environmental variables at multiple scales were related to fish assemblage structure. The dominant environmental gradient influencing functional and taxonomic structure of fish communities (highest correlations with RLQ axis 1) separated sites according to latitude, elevation and climate, factors that are spatially intercorrelated within the Grijalva Basin. Important local-scale environmental differences among sites also occurred along this gradient and appeared to influence assemblage structure. These local factors were substrate type and presence of pool habitats, with streams further downstream in the fluvial gradient characterized by rockier substrates and wider, deeper pools. Other important local-scale environmental influences revealed by the RLQ analysis included the amount of in-stream structure, number of riffles, stream depth, and canopy cover. The amount of forest in the watershed was correlated with these variables, and likely influenced channel canopy cover and the amount of in-stream cover provided by woody debris. Stream width and

abundance of aquatic macrophytes were negatively correlated with these variables and also were strongly associated with fish assemblage structure.

The PCA based on species traits revealed that principal functional differences among species were associated with locomotion and habitat use (fin lengths, body depth, caudal peduncle dimensions), trophic ecology (gill raker length, snout length and protrusion, head length, eye diameter, gut length) and life-history strategy (egg diameter, clutch size). Results of the RLQ analysis showed that differences in the trait composition of local assemblages were related to environmental differences among stream sites. Small, high-elevation streams lacking pool habitats contained fish species with more streamlined bodies. This was consistent with expectations based on the RHT (Townsend and Hildrew 1994), which predicts that fishes with more streamlined body shapes will be abundant in high-elevation streams because these forms are more resistant to fluctuating hydrology typical of headwater streams. Streams at lower elevations in the fluvial gradient tended to have more pool habitat and deeper channels, experienced more rainfall, and tended to contain fishes with longer fins, longer gill rakers, deeper bodies, and larger eyes. Gill raker length is associated with filter feeding in fishes (Gatz 1979), which is expected to be more common in downstream reaches based on the RCC and findings of Poff and Allan (1995). Species with deeper bodies and longer fins are expected to be common in lowland streams with more pool habitats because such traits are associated with fine-scale maneuvering in low-velocity habitats (Gatz 1979, Webb 1984). Lamouroux et al. (2002) also found that in Europe and North America, stream reaches with more pool habitats supported proportionally more species with deep, non-streamlined bodies. This suggests an important role for reach-scale filtering of traits by hydrological and geomorphological characteristics as described by Poff (1997).

Species occurring in streams with greater in-stream structure, deeper channels, greater canopy cover, and more forested watersheds had larger eggs and smaller clutch sizes. This pattern in reproductive traits corresponded with RLQ axis 2, and there was no clear relationship between these traits and the overall fluvial gradient (RLQ axis 1). Thus, RHT predictions of larger clutch size and smaller egg size (traits often associated

with demographic resilience; but see discussion of the periodic life history strategy in Winemiller and Rose 1992, Winemiller 2005) in upstream reaches were not confirmed. The lack of a clear relationship between reproductive traits and position in the watershed was likely due to the widespread distribution of poeciliid species, live-bearing fishes with large eggs and small clutch sizes, throughout the entire basin. Fishes with long intestines were more abundant in wider streams with open canopies and more abundant aquatic macrophytes. Long intestines in fishes are associated with herbivory and detritivory (Gatz 1979), which are expected to be more common in lowland streams according to the RCC (Vannote et al. 1980) and have been shown to increase with stream size (Goldstein and Meador 2004). Though this trait was not highly correlated with the latitude/elevation gradient, it was associated with habitat characteristics (i.e., wide channels, low canopy cover, high in-stream productivity) typical of streams lower on the river continuum (Vannote et al. 1990). Thus, this pattern partially confirms expectations of the RCC and suggests the action of reach-scale filters via riparian characteristics and in-stream production.

In general, the functional trait-space occupied by fish assemblages increased in stream reaches located further downstream along the Grijalva fluvial gradient. The RHT suggests that assemblage-wide diversity of functional traits should increase from upstream to downstream as streams become more stable and a greater diversity of habitats is available for refugia from disturbance (Townsend and Hildrew 1994). This also confirms RCC expectations that functional diversity should increase in lower reaches within a drainage basin as increasing diversity of resources promotes trophic diversity of fishes (Thorp et al. 2008). The lower reaches of large rivers, such as the Grijalva, typically have lower gradients with broad and meandering channels that interconnect and exchange materials and organisms with aquatic floodplain habitats that are spatially heterogeneous and temporally dynamic. As a result, these lower reaches tend to provide more diverse habitats and food resources and more aquatic production due to the greater size of the ecosystem and reduced effects of hydraulic disturbance (Thorp et al. 2008). Total trait space occupation also generally increased with species

richness along the Grijalva fluvial gradient, a pattern shown in studies that have compared fish assemblages within river basins (e.g., Hoagstrom and Berry 2008) and among basins across biogeographic regions (e.g., Winemiller 1991).

In summary, I found that environmental variables at local and landscape-scales were related to the functional structure of stream fish assemblages in the Grijalva Basin. I observed an increase in functional diversity along with increasing species richness from the highlands to the lowlands along the fluvial gradient of the watershed. These results provide support for some aspects of the RCC, RHT, and landscape filtering conceptual frameworks for trait-environment relationships in stream fish assemblages. The incorporation of a functional trait approach should make the results of this study applicable to research on fish assemblages in other rivers, including those in biogeographic regions with very different taxa and greater species richness. Compared to studies that focus on taxonomic identity, research that analyzes functional trait diversity should translate better across regions and thus provide opportunities to discover general ecological patterns (Poff 1997, Poff et al. 2006, Olden et al. 2010). Moreover, improved knowledge of how functional traits of fishes respond to natural environmental gradients will greatly enhance our ability to predict the manner in which local species assemblages are likely to respond to human-induced environmental changes.

CHAPTER III

CHANGES IN TROPHIC STRUCTURE OF STREAM FISH ASSEMBLAGES ALONG THE LONGITUDINAL FLUVIAL GRADIENT OF THE RIO GRIJALVA, MEXICO

Introduction

Ecologists have long recognized that ecosystem processes and biological community structure change along fluvial gradients within river basins (e.g., Hynes 1970, Horwitz 1978, Vannote et al. 1980). Patterns of discharge, availability of production sources, and species interactions differ along with abiotic environmental characteristics that transition from headwaters to downstream reaches. The trophic structure of aquatic communities also is expected to change along the course of a river basin from upstream tributaries to lowland streams (Vannote et al. 1980, Schlosser 1987, Power and Dietrich 2002). The River Continuum Concept (RCC) relates changes in environmental factors such as stream size and riparian characteristics that occur along longitudinal fluvial gradients to changes in availability of food resources. In turn, these shifts are expected to influence the trophic structure of stream assemblages. With respect to fishes, generalized invertebrate feeders are expected to predominate in headwater reaches where in-stream algal production is lower and narrow channels with less predictable flow limit the diversity of prey items. Omnivores, detritivores, herbivores, and piscivores are predicted to become more abundant in streams further downstream in a river basin as in-stream production, stable flow and diverse habitats provide for a more diverse resource base (Vannote et al. 1980, Schlosser 1987).

Changes in the diversity and species composition of fish assemblages have been observed along longitudinal gradients in many temperate and tropical watersheds (e.g., Ibarra and Stewart 1989, Rahel and Hubert 1991, Osborne and Wiley 1992, Edds 1993, Hoeinghaus et al. 2004). Studies examining the abundance of trophic groups along large fluvial gradients have generally supported expectations of the RCC. For example, Schlosser (1982) found that larger, more temporally stable lowland streams with larger

pool habitats supported more insectivorous and piscivorous fishes while smaller, less stable headwater streams contained mostly generalist species. Poff and Allan (1995) also found that hydrologically variable streams were more likely to contain trophic generalists. Ibañez et al. (2007) found that the proportion of invertebrate feeders decreased while the proportion of omnivores, herbivores and piscivores increased from upstream to downstream reaches in African streams. Examining a gradient of stream size, Goldstein and Meador (2004) observed in increase in herbivores and planktivores in larger streams and rivers.

The goal of this research was to examine changes in the trophic structure of stream fish assemblages from the highlands to the lowlands along the fluvial gradient of the Río Grijalva Basin of southern Mexico. Few studies have explicitly examined food resource use in fish assemblages across large tropical watersheds, and little is known about the basic ecology of Río Grijalva fishes. In order to identify patterns in trophic structure of Grijalva fish assemblages, we analyzed stomach contents of fishes in stream reaches spanning the entire basin from headwater tributaries to lowland streams. Specifically, our objectives were to examine how the abundance of trophic guilds, diversity of food resource use, and dietary niche overlap within local fish assemblages change along the fluvial gradient of the Río Grijalva basin.

Methods

Study region description

The Río Grijalva begins in Guatemala and flows through the states of Chiapas and Tabasco in southern Mexico. As the Grijalva nears the Gulf of Mexico in Tabasco, it joins the Río Usumacinta, and together they form the largest river in Mesoamerica. Approximately 115 species from 31 families have been documented in the region, and an estimated 36% of species are endemic (Miller 2005). This study focuses on wadeable streams within the Grijalva basin above its confluence with the Río Usumacinta, an approximately 60,000-km^2 region (Figure 1). The environmental characteristics of stream habitats within the Grijalva basin change markedly along a longitudinal gradient

from the mountainous Sierra Madre de Chiapas to the coastal plains in Tabasco. Upland, high-gradient streams in the headwaters give way to broad and sinuous channels in the middle sections, and ultimately the channels are transformed into a mosaic of wetlands before draining into the Gulf of Mexico (Hudson et al. 2005). Upland stream habitats are more environmentally harsh, with high temporal variation in flow, less spatial heterogeneity and fewer low-velocity microhabitats in local communities. Further downstream on the fluvial gradient, stream habitats become progressively more stable, with more low-velocity pools, more structurally complex microhabitats, and a broader prey resource base. I designated the area above the Angostura reservoir as the "Upper Grijalva," the portion of the watershed below Angostura and above the Malpaso reservoir as the "Middle Grijalva," and the section below Malpaso to the confluence with the Río Usumacinta as the "Lower Grijalva." I conducted our study in 20 streams across a range of environments within the Grijalva watershed. The study sites were selected to ensure roughly equal representation in upper, middle, and lower portions of the basin with data from a range of stream orders (from small headwaters to broad, high-order, major tributaries).

I sampled the 20 streams during March and April of 2008 and 2009. These months are within the dry season for this region, a time when flows are lower and fish can be captured more efficiently. At each survey site, a 200-m stream reach encompassing all available macrohabitat types (e.g., pools, runs, and riffles) was designated for fish collection and local habitat measurements. Within each study reach, fishes were collected by performing a minimum of six seine hauls of 10-m (seine dimensions = 5 x 2 m, 5-mm mesh). Where appropriate, sampling was supplemented using a cast net (2 m diameter, 1-cm mesh). In sites with rocky substrate where seining was inefficient, fishes were sampled using a backpack electrofisher (Smith-Root Model LR-24). Electrofishing was performed with a single pass moving upstream across the entire study reach. Collected fishes were identified, counted, and either released into the habitat or preserved in 10% buffered formalin for later identification. Preserved fishes

were deposited in the museum collection of El Colegio de la Frontera Sur in San Cristobal de las Casas, Chiapas.

For each stream assemblage, I examined stomach contents of five to ten adult specimens of each fish species. Volumetric proportions of stomach contents were estimated following the methods of Winemiller (1990). Fishes consumed were identified to species when possible, and invertebrates were identified to order. Prey items were grouped into 12 broad categories prior to statistical analyses. These categories were: fishes, molluscs, diptera, ephemeroptera, odonata, trichoptera, other aquatic insects, benthic meiofauna, terrestrial insects, terrestrial vegetation, algae, and detritus.

Statistical analyses

Principal components analysis (PCA) was performed on the dietary dataset to identify primary gradients in trophic resource use among species and stream sites. The PCA was performed using the mean proportional volumes of the 12 diet categories for each species at each stream site. Scores on the first six PC axes were used to estimate the multivariate volume of trophic space occupied by the assemblages. This volume was calculated using the convex hull volume method of Cornwell et al. (2006). These calculations were performed with the Quickhull algorithm (Barber et al. 1996) in MATLAB software (Mathworks Inc., 2009). Linear regressions were used to examine relationships between the trophic space occupied by assemblages and species richness, functional trait diversity (calculated in Chapter II), and position along the Grijalva fluvial gradient. Pianka's (1973) symmetrical index of niche overlap was calculated as a measure of dietary similarity between species within assemblages using volumetric proportions of the 12 aggregated prey categories. Niche overlap values may range from 0 to 1, with higher values indicating more complete overlap.

I used hierarchical cluster analysis to produce a dendrogram of trophic similarity among species based on volumetric proportions of the 12 prey categories. A similarity matrix was constructed using the Bray-Curtis index and Ward's algorithm was used for

linking of clusters. Based on the results of the cluster analysis, species were assigned to five trophic groups: piscivores, benthic invertebrate feeders, surface invertebrate feeders, omnivores, and detritivore/algivores (Table 3). I then quantified among-site differences in trophic group composition by performing non-metric multidimensional scaling (NMS) on log-transformed trophic group abundances. I used Bray-Curtis dissimilarity (BCD) as the distance measure, and retained a two-dimensional solution as the stress value (a measure of agreement between BCDs and the configuration of the ordination) was relatively low and did not substantially decrease when additional axes were included in ordination.

Table 3. Trophic group assignments and regional affiliations of Río Grijalva species captured in this study.

Family	Species	Trophic Group	Region		
			Upper	Middle	Lower
Clupeidae	*Dorosoma petenense*	Detritivore/algivore		X	X
Characidae	*Astyanax aeneus*	Omnivore	X	X	X
	Brycon guatemalensis	Omnivore	X	X	X
Heptapteridae	*Rhamdia guatemalensis*	Benthic invert. feeder	X	X	X
	Rhamdia laticauda	Benthic invert. feeder		X	
Atherinopsidae	*Atherinella alvarezi*	Omnivore		X	X
Poeciliidae	*Belonesox belizanus*	Piscivore			X
	Carlhubbsia kidderi	Detritivore/algivore			X
	Heterandria bimaculata	Surface invert. feeder			X
	Heterophallus milleri	Surface invert. feeder			X
	Poeciliopsis fasciata	Omnivore	X	X	
	Poeciliopsis hnilickai	Detritivore/algivore	X		
	Poeciliopsis pleurospilus	Detritivore/algivore	X	X	
	Poecilia mexicana	Detritivore/algivore			X
	Poecilia sphenops	Detritivore/algivore	X	X	
	Priapella chamulae	Surface invert. feeder			X
	Priapella compressa	Surface invert. feeder			X
	Xiphophorus hellerii	Detritivore/algivore		X	X
Profundulidae	*Profundulus labialis*	Omnivore	X	X	
	Profundulus punctatus	Omnivore	X	X	
Cichlidae	*Amphilophus macracanthus*	Benthic invert. feeder		X	
	Cichlasoma grammodes	Benthic invert. feeder	X	X	
	Cichlasoma salvini	Benthic invert. feeder		X	X
	Cichlasoma trimaculatum	Benthic invert. feeder		X	
	Oreochromis sp.	Detritivore/algivore	X	X	
	Theraps lentiginosus	Benthic invert. feeder			X

Table 3. Continued.

Family	Species	Trophic Group	Region		
			Upper	Middle	Lower
Cichlidae	*Thorichthys helleri*	Benthic invert. feeder		X	X
	Thorichthys meeki	Benthic invert. feeder			X
	Thorichthys socolofi	Benthic invert. feeder			X
	Vieja bifasciata	Detritivore/algivore			X
	Vieja hartwegi	Omnivore	X	X	
	Vieja intermedia	Detritivore/algivore			X

Results

A total of 33 species were collected from the streams sampled in our study region. Local stream fish assemblages were dominated by the Cichlidae and Poeciliidae, the two families that dominate the freshwater ichthyofauna of Mesoamerica overall. Non-native tilapia (*Oreochromis* species, family Cichlidae) were present at five sites in the Middle Grijalva region. Examination of stomach contents revealed that throughout the watershed, fishes consumed aquatic insect larvae, algae, and detritus (Figure 8). Aquatic insects made up the largest proportion of overall assemblage resource use in all three sections of the Grijalva. A few species, including *Cichlasoma grammodes*, *Cichlasoma trimaculatum*, *Astyanax aeneus*, and *Rhamdia guatemalensis* consumed fishes as part of their diet, but only one species, *Belonesox belizanus*, was a specialized piscivore (Table 3).

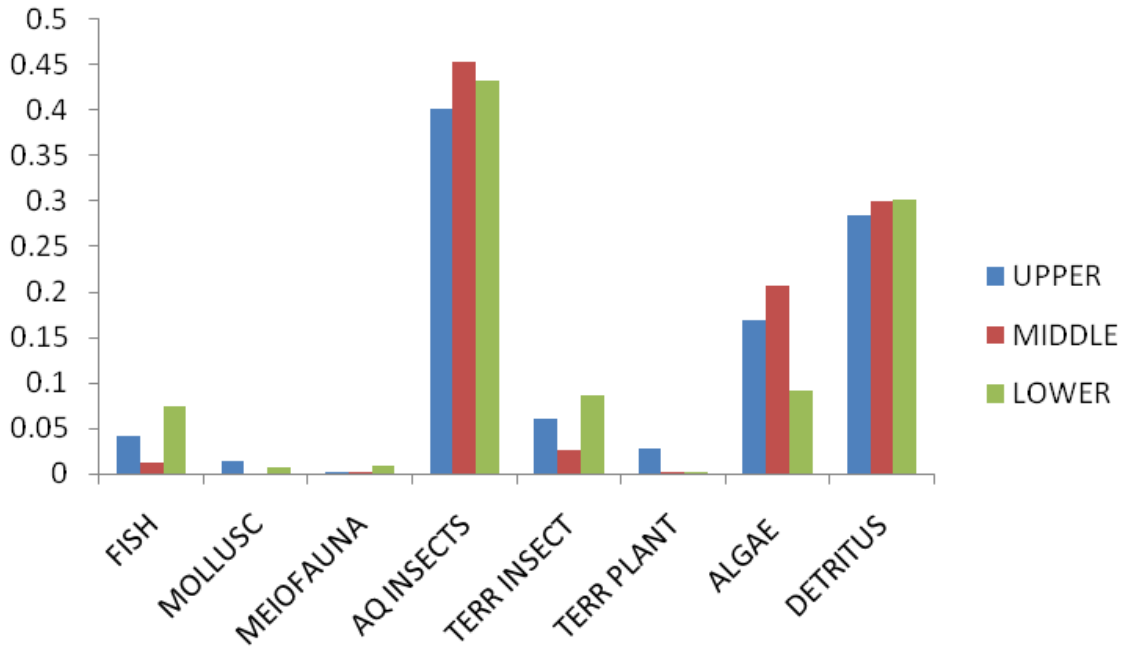

Figure 8. Average volumetric proportions of eight broad trophic resource categories for assemblages in the Upper, Middle, and Lower Grijalva regions.

The first six axes of the PCA of volumetric proportions of food resources explained 70.8% of variation among species at the 20 sites. The dominant gradient (PC1, 20.4% of variance) was most strongly associated with the proportion of detritus, diptera larvae, ephemeroptera larvae, and other aquatic insects in the diet (Figure 9). Detritivorous species, such as *Poecilia*, *Poeciliopsis pleurospilus*, and *Vieja* species had low scores on axis 1. *Thorichthys* species, *Theraps lentiginosus*, and other cichlids consuming mostly benthic insects had high scores on axis 1. Assemblages within all three regions contained species broadly distributed along axis 1. The second axis (PC2, 12.6% of variance) contrasted species consuming terrestrial insects and fish versus those with more algae and small invertebrates in their diet. Omnivorous species such as *Atherinella alvarezi* and *Profundulus* species plotted high on axis 2. *Astyanax aeneus*, *Heterandria bimaculata*, and other species with a large proportion of ants and other

terrestrial insects in their diet had low scores on axis 2. Species in Lower Grijalva assemblages showed the highest dispersion along axis 2.

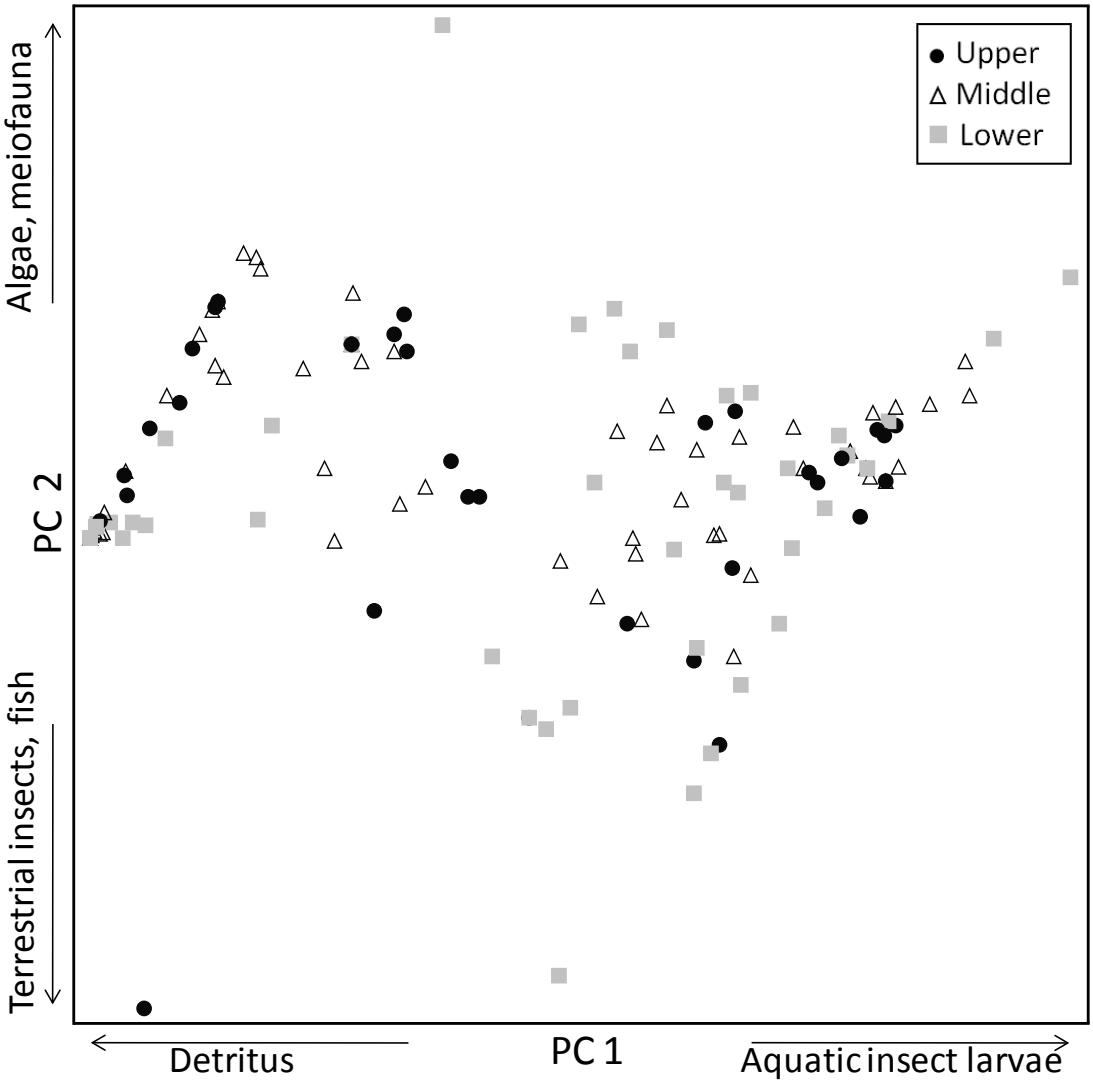

Figure 9. PCA ordination of Río Grijalva species based on proportional volume of prey items in stomach contents. Each point represents the position of a species at a particular local assemblage.

The volume of trophic space occupied by fish assemblages generally increased along with species richness from the highlands in the south to the lowlands in the north on the fluvial gradient of the Grijalva Basin (Figure 10). Sites with the largest convex hull volumes of trophic space were in the Lower Grijalva region. Streams with similarly high species richness in the Middle Grijalva consumed a less diverse set of food resources, indicating that environmental differences and faunal shifts in the region affected the trophic diversity of fish assemblages. Some sites in the Upper and Middle Grijalva had high trophic diversity despite containing relatively few fish species. These sites contained species that consumed distinctive resources. For example, *Vieja hartwegi* and *Brycon guatemalensis* in the Río Legartero (Upper Grijalva) consumed large quantities of snails and terrestrial fruit respectively, resources that were rarely consumed in other assemblages. These patterns in trophic space occupation correspond with trends observed for functional trait occupation along the fluvial gradient of the Grijalva (Chapter II).

On average, niche overlap was high among species in streams of the Río Grijalva basin. No significant relationship between average niche overlap and position along the fluvial gradient was observed (Figure 10). Niche overlap was highest in Middle Grijalva stream reaches. In this region, the broad stream channels had relatively low riparian cover and filamentous algae was very abundant at most sites. Filamentous algae was a component in most species' diets in this region, leading to greater overall overlap among species. The total number of prey categories consumed within assemblages was also generally lower in the Middle Grijalva region.

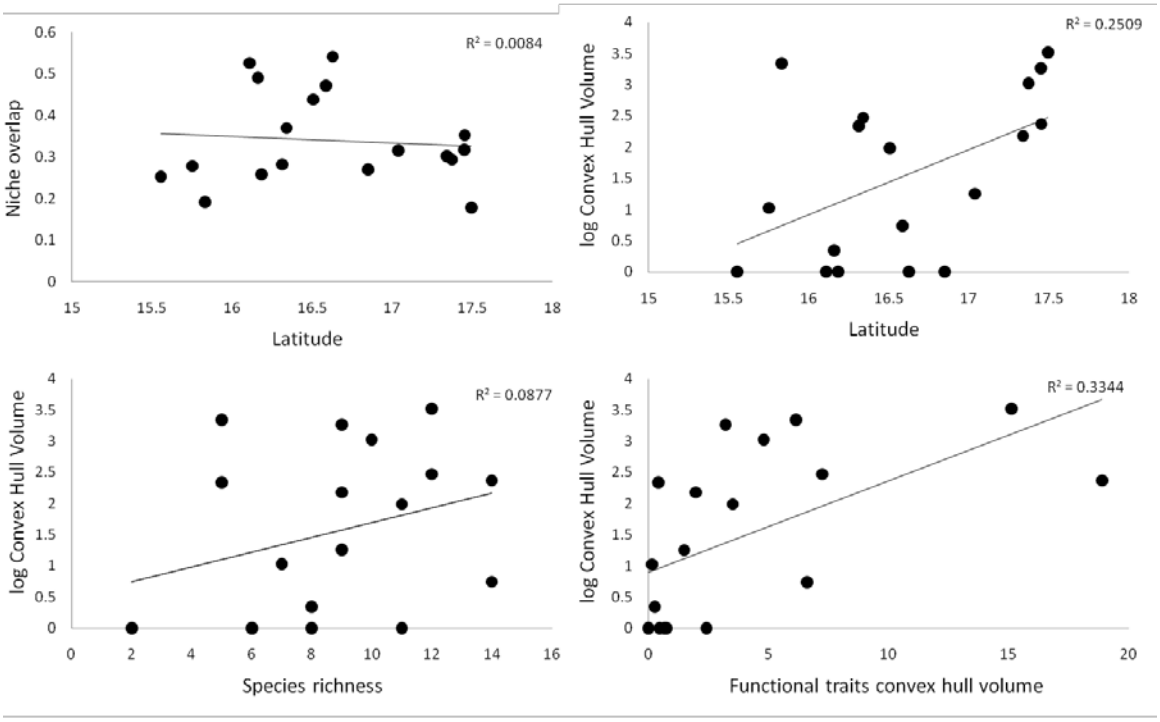

Figure 10. Regression of dietary niche overlap and volume of trophic space occupation of Río Grijalva fish assemblages on latitude. Latitude corresponds to a great extent with the fluvial gradient of the Río Grijalva, which flows from south to north.

The NMS analysis identified two axes that explained 82.7% of the variance in abundance of trophic groups among sites (Figures 11 and 12). The dominant axis (NMS 1, 72.7% variance) separated sites containing all or most trophic groups (low scores on axis 1) from those dominated by generalist omnivores (high scores on axis 1). Assemblages in the Lower Grijalva had greater diversity of trophic groups and plotted on the left side of axis 1. Piscivores and surface invertebrate feeders were only present in these sites. Assemblages with the lowest diversity (of species and trophic groups) in the Middle and Upper Grijalva plotted on the right side of axis 1. Axis 2 (10.0% variance) contrasted sites with the more rare trophic groups (piscivores and surface invertebrate feeders) from sites containing only omnivores, detritivore/herbivores, and

benthic invertebrate feeders. High-diversity Lower Grijalva assemblages had high scores on axis 2.

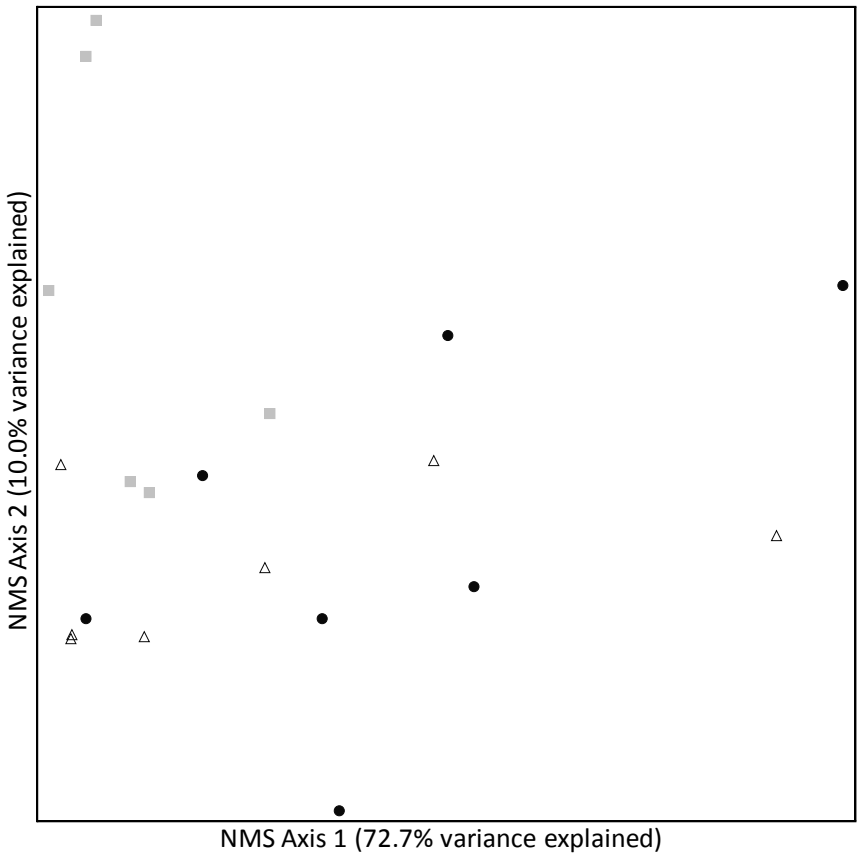

Figure 11. NMS ordination of Río Grijalva stream reaches based on trophic group composition of fish assemblages.

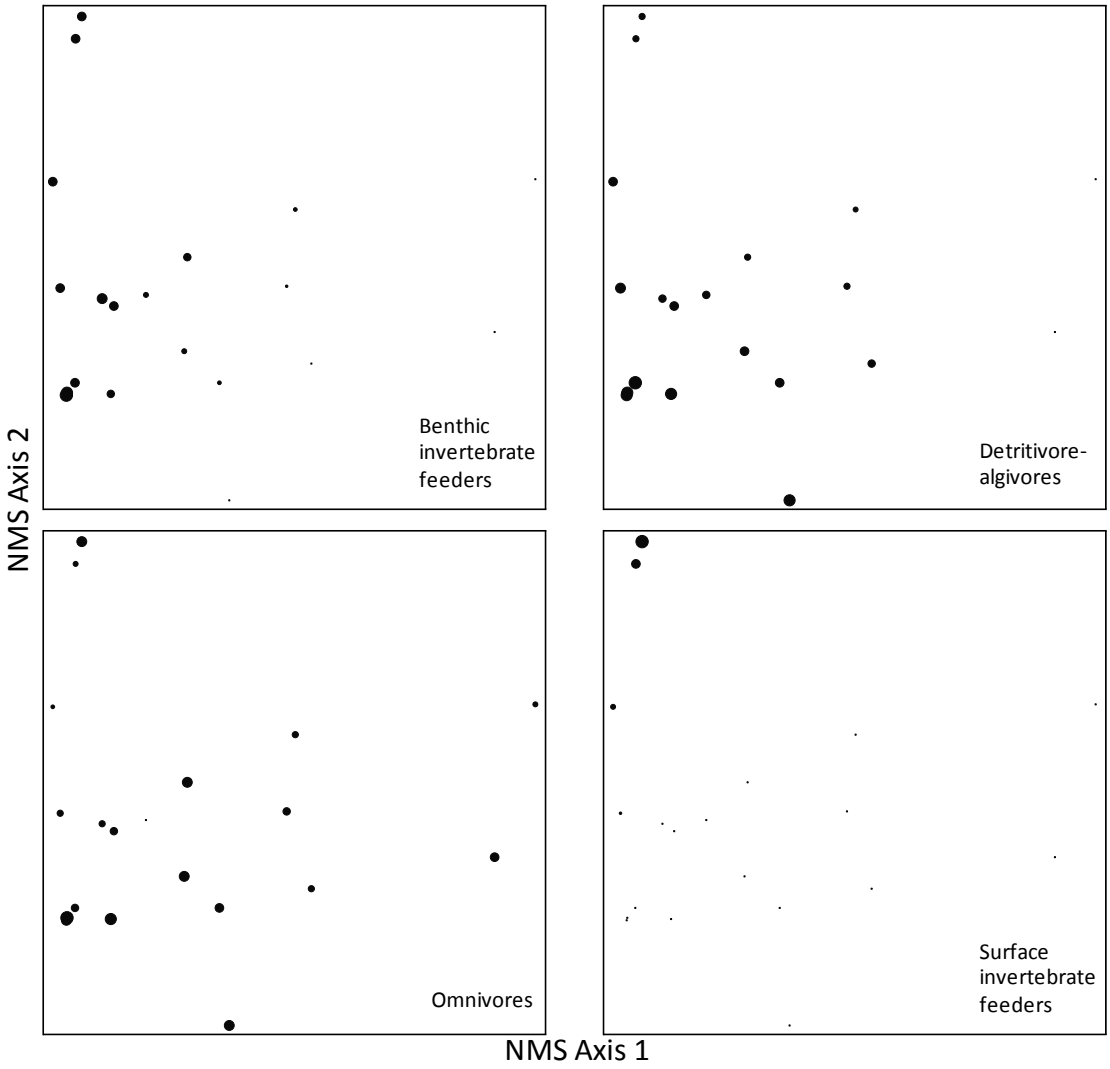

Figure 12. NMS ordination of Río Grijalva fish assemblages (as in Figure 11) showing the abundance of trophic groups. Size of the symbols represents the abundance particular trophic groups at stream sites.

Discussion

Longitudinal changes in fish species richness and taxonomic composition are common in most large river basins (Matthews 1998). Concomitant with these changes, the trophic structure of fish assemblages has been shown to vary along fluvial gradients in temperate and tropical watersheds (e.g., Schlosser 1982, Poff and Allan 1995, Ibanez

et al. 2007, Winemiller et al. 2010). Similarly, we observed changes in trophic structure as resource use and the abundance of trophic groups shifted from the uplands to the lowlands of the Río Grijalva basin. In stream assemblages of the Upper Grijalva, fishes were mostly generalist omnivores, feeding on benthic invertebrates, algae and detritus. In the Middle Grijalva, fishes were also mostly generalists, but the overall diversity of resources used was generally lower and dietary niche overlap was highest. Middle Grijalva assemblages with the lowest trophic space occupation and highest niche overlap were in watersheds draining the more arid, more developed, and less forested region in western Chiapas near the city of Tuxtla Gutierrez. Streams within less forested landscapes generally support less diverse invertebrate assemblages (e.g., Urban et al. 2006), so the invertebrate resource base in this region is likely narrower than in the mesic, forested zones in the Upper and Lower Grijalva basin. Further downstream in the lowlands, more specialized feeding became more common, with greater abundances of piscivores, surface invertebrate feeders, and detritivore/algivores.

The shift from trophic generalists to more specialized fish assemblages with a corresponding increase in the diversity of food resources used from the uplands to the lowlands of the Grijalva fluvial gradient is consistent with RCC expectations (Vannote et al. 1980) and studies in other regions (e.g., Horwitz 1978, Schlosser 1982, Poff and Allan 1995, Pouilly et al. 2006). As expected, trophic diversity was highest in lowland streams, where fish species richness and functional trait diversity were highest (Chapter II), and more stable habitats and greater spatial heterogeneity provide for a broad prey resource base (Horwitz 1978, Schlosser 1987). This diversity decreased in assemblages further upstream, where the flow regime is harsher and fewer favorable habitat types are available for fishes or their prey resources.

Previous studies of fish assemblage trophic structure along fluvial gradients have found a general decrease in the proportion of invertebrate feeders in downstream reaches (e.g., Oberdorff et al. 1993, Pouilly et al. 2006, McGarvey and Hughes 2008, Ibanez et al. 2007). In this study, I found that the proportion of aquatic invertebrates in the diets of fishes remained fairly constant throughout the watershed. The abundance of

invertebrate feeders was highest in downstream reaches, where cichlids specializing on benthic invertebrates (e.g., *Thorichthys* species) and poeciliids feeding on invertebrates at the surface (e.g., *Priapella* species) were common. Goldstein and Meador (2004) also found that the proportion of invertebrate feeding did not decline in downstream reaches as would be predicted based on the RCC. Citing the flood-pulse concept (Junk et al. 1989) and Thorp and Delong's (1994) riverine productivity model, they suggest that limited variation in the consumption of invertebrates along longitudinal gradients may be related to the importance of aquatic-terrestrial linkages throughout large river basins. In other regions, an increase in piscivory has been observed in streams further downstream on longitudinal gradients (e.g., Horwitz 1978, Pouilly et al. 2006, Ibanez et al. 2007, McGarvey and Hughes 2008). Specialized piscivory was rare in Grijalva streams, and *Belonesox belizanus*, found in the Lower Grijalva, was the only species collected that fed principally on fishes. *Astyanax aeneus* and the cichlid species *Cichlasoma grammodes* and *Cichlasoma trimaculatum* regularly consumed fishes along with invertebrates, and these species were found in the Middle and Upper Grijalva regions. Thus, specialized piscivory was only found in the lowlands, but the proportion of fish as a dietary resource did not increase substantially downstream. Contrary to RCC expectations and findings in other rivers (e.g., Schlosser 1987, Goldstein and Meador 2004), algae and detritus were consistently important components of the diet throughout the watershed. The proportion of strict algivore/detritivores increased downstream as in other regions (e.g., Goldstein and Meador 2004, Pouilly et al. 2006), but omnivorous fishes like *Profundulus* species and *Astyanax aeneus* consumed large proportions of these resources even in the uppermost tributaries sampled. Similarly, Ibañez et al. (2009) found that in contrast to relationships reported for temperate streams, there was no significant increase in herbivorous or detritivorous fishes further downstream on fluvial gradients in tropical regions of South America and Africa. They suggested that this may be due to greater energy input supporting higher autochthonous productivity in tropical food webs (Davies et al. 2008).

In summary, the results of this study support some general expectations regarding shifts in functional structure along the longitudinal gradients of large river basins. In some cases, however, observed patterns differed from previous studies and theoretical expectations. Many factors that influence stream fish community structure do not vary predictably along river continua. For example, urban development, deforestation, and introduced species are anthropogenic disturbances that may have a profound influence on stream fish assemblages regardless of longitudinal position. In this region, stream reaches in the more developed watersheds in the Middle Grijalva region had the lowest trophic diversity, confounding the expected relationships between resource use and position on the fluvial gradient. Additionally, patterns in our study region may have differed from RCC expectations due to overall differences in food web properties between temperate and tropical regions (Davies et al. 2008, Winemiller et al. 2008). These results highlight the need to evaluate patterns of functional assemblage structure along longitudinal gradients of rivers in varying biogeographic regions, climates, and levels of anthropogenic disturbance.

CHAPTER IV

FUNCTIONAL TRAIT DIVERSITY AND TRAIT-ENVIRONMENT RELATIONSHIPS IN CENTRAL TEXAS STREAM FISH ASSEMBLAGES: IMPLICATIONS FOR BIOMONITORING

Introduction

Ecologists and natural resource managers tasked with monitoring stream ecosystems are keenly interested in establishing ways to gauge stream health based on the composition of local species assemblages. Metrics such as the index of biotic integrity (IBI) proposed by Karr et al. (1986) use trophic guilds and other attributes of species assemblages as indicators of the ecological state of streams. These indices score stream reaches based on the abundance of taxa that have been assigned to particular categories based on feeding ecology, habitat use, and sensitivity to anthropogenic disturbance. In order to account for zoogeographic differences, such indices must be adjusted for different regions. Identifying relationships between environmental conditions and stream fish assemblages that translate across regions remains a key challenge.

Previous studies of environmental influences on stream fish community structure have revealed several general patterns. For example, Schlosser (1982) found that larger, more temporally stable streams with larger pool habitats supported larger, insectivorous and piscivorous fishes while smaller, less stable streams contained smaller, generalist species. Similarly, Poff and Allan (1995) found that the proportion of trophic specialists in fish assemblages was greater in more hydrologically stable streams. Other studies have shown that at the landscape scale, agriculture and other land use in a watershed can affect the composition of local fish assemblages. For example, Walser and Bart (1999) observed a reduction in fish species associated with coarse substrate in stream reaches where agriculture in the landscape led to increased silt and decreased complexity in substrate composition. Regional land use for agriculture and urban development has

also been correlated with a decrease in species considered intolerant to anthropogenic disturbance (e.g., Roth et al. 1996, Brown 2000, Wang et al. 2001).

Documenting the relationships between environmental variables and species traits related to resource use, habitat preference, movement, and life history can potentially improve upon traditional analyses based on taxonomic structure. Such approaches may reveal more general patterns applicable across geographic scales (Lamouroux et al. 2002, McGill et al. 2006, Poff et al. 2006). Whereas the occurrence of certain taxa in a local assemblage may reflect historical influences in addition to environmental factors, the functional composition of an assemblage more closely reflects constraints imposed by environmental gradients (Schlosser 1982, Poff and Allan 1995, Angermeier and Winston 1999). Functional-trait approaches may also improve upon methods such as the IBI that use functional grouping. Extensive studies on the ecomorphology (e.g., Gatz 1979, Webb 1984, Sibbing and Nagelkerke 2001) and life histories (e.g., Balon 1975, Winemiller and Rose 1992) of stream fishes have yielded a great deal of information on traits that can be used to make inferences about the ecology of fish species. Examining these traits may reveal finer functional differences between species that might not be apparent when species are assigned to general functional categories (Fonseca and Ganade 2001, Villeger et al. 2008). The use of a broad suite of traits allows for characterization of multiple niche dimensions of a species, while functional groups usually focus on particular aspects such as trophic ecology, reproductive strategy, or habitat use (Wilson 1999). Another advantage of using quantitative traits is that they can readily be used for new multidimensional methods of estimating functional diversity (e.g., Villeger et al. 2008, Laliberte and Legendre 2010).

Though many studies have applied functional trait approaches to stream invertebrate assemblages (e.g., Statzner et al. 2001, Doledec et al. 2006, Poff et al. 2006), our understanding of trait-environment relationships for stream fishes requires further development (Lamouroux et al. 2002, Olden et al. 2010). The river habitat template (RHT) proposed by Townsend and Hildrew (1994) provides a key framework for general trait-environment relationships for stream communities. According to the

RHT, temporal variability and spatial heterogeneity influence traits related to resistance and resilience of stream organisms. For example, small fishes with short reproductive cycles are expected to be more abundant in streams with flashy flow regimes and narrow channels with low habitat heterogeneity. Observed relationships between species traits and physical habitat have not consistently matched predictions of the RHT, however (e.g., Persat et al. 1994, Resh et al. 1994, Merigoux et al. 2001). Lamouroux et al. (2002) suggested that the mismatch may be due to the effects of environmental filters above the reach scale (Poff et al. 1997), the influence of evolutionary history (e.g., Moyle and Herbold 1987), or alternative strategies for adaptation to environmental conditions (Resh et al. 1994). Studies incorporating environmental variables at multiple scales with more comprehensive suites of traits can potentially reveal relationships that improve the predictive power of habitat templates (Lamouroux et al. 2002).

In this study, I examined the influence of environmental variables at local and landscape scales on the functional structure of stream fish assemblages in a large region of Central Texas. Prior research in this region has shown that the taxonomic structure of these assemblages is related to local, in-stream habitat features such as substrate type, abundance of woody debris, and presence of riffles, as well as the extent of development for urban and agricultural uses at the landscape scale (Winemiller et al. 2009). Here my objectives were to identify associations between functional traits of species and environmental variables at multiple scales within the region and to examine relationships between functional diversity of fish assemblages, environmental gradients, and established measures of habitat quality and biotic integrity. These relationships may provide valuable information for determining the potential use of functional traits of fish assemblages as a means of monitoring the environmental quality of streams.

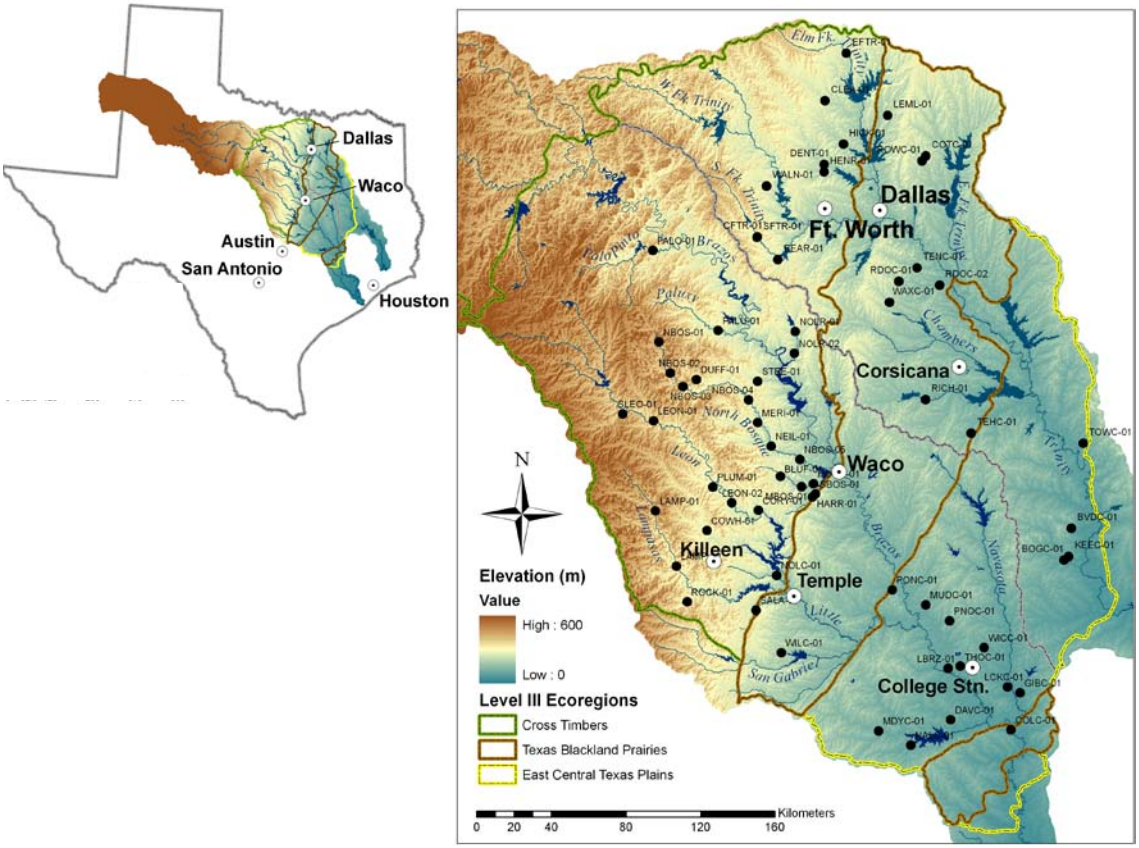

Figure 13. Map of study region in the Brazos and Trinity Basins of Texas (adapted from Winemiller et al. 2009). Solid dots indicate locations of surveyed stream reaches.

Methods

Study area

Data were collected from 64 perennial, wadeable streams within the Brazos and Trinity River basins in Texas (Figure 13). These streams lie within the Cross Timbers, Blackland Prairies, and East Central Texas Plains ecoregions. The Cross Timbers ecoregion, a mosaic of forests, woodlands and prairies, currently is dominated by rangelands but also includes several major urban centers. The Texas Blackland Prairies ecoregion is distinguished from neighboring regions by having fine-textured, clay soils and less forest cover. This region was historically tallgrass prairie and now contains a higher percentage of cropland than adjacent ecoregions. Large areas within the

Blackland Prairies ecoregion are being converted to urban and industrial uses. The East Central Texas Plains ecoregion was historically covered by post oak savanna and currently is dominated by rangelands, but also contains row crops and urban development (Griffin et al. 2004). Study sites were selected to provide broad geographic coverage, a range of landscape features (including land use), and representation of a range of stream habitat conditions.

Data collection

I sampled the streams during the summer (June-August) of 2008. At each survey site, a 160-500 m stream reach was designated for fish collection and local habitat measurements. Reach length was determined based upon the wetted width of the stream (approximately 40 times the average width). Within each study reach, all available habitats were sampled using a backpack electrofisher (Smith-Root Model LR-24) and seine net (4.6m x 1.8m or 1.8m x 1.8m, 5-mm mesh). Crews of 3-4 people electrofished each study reach in a single upstream pass with a minimum effort of 900 seconds. The reach was then sampled with a seine net with a minimum of six 10-m hauls. If the sixth haul yielded additional species in the sample of all available mesohabitats within the study reach, additional seine hauls were made until no additional species were captured. Collected fishes were identified, separated into juvenile and adult age classes, counted, and either released into the habitat or preserved in 10% buffered formalin for later identification. Numerical abundance of each fish species was recorded for each study reach and sampling event for analyses of patterns in fish community structure.

At each study site, I measured 57 local habitat variables (Table 4) including substrate composition, in-stream cover, wetted width, depth, canopy cover, bank slope, riparian buffer width, instantaneous dissolved oxygen, conductivity, and pH on the same dates as fish sampling. I made these measurements at 5 to 6 evenly spaced transects (depending on reach length). Some measurements, such as number of riffles, maximum pool depth, stream sinuosity, and composition of riparian vegetation, were summarized for the entire study reach. Discharge (in m^3/s) was also measured along a representative

transect within each reach using a portable electromagnetic flow meter (Marsh-McBirney Flo-Mate Model 2000).

Twenty-two landscape-scale variables describing spatial relationships (coordinates), physical characteristics and topography, land use, and distribution of disturbance points (outfalls and dams) were calculated for each site (Table 5). Watershed boundaries for each sample site were automatically digitized in ArcGIS 9.2 with the ArcHYDRO 9 extension using a 1:24,000 scale digital elevation model (DEM) expressed as a 30 m raster, available from the U. S. Geological Survey. Mean slope and elevation were calculated for each watershed using the digital elevation model. Mean annual precipitation was calculated for each watershed from polygon coverage of average monthly and annual precipitation for the climatological period 1961-90. This dataset was obtained from USDA-NRCS. Number of wastewater outfalls and cumulative outfall (mgd) were calculated for each watershed based on the Texas Commission on Environmental Quality (TCEQ) municipal and industrial wastewater outfall shapefile available from http://www.tceq.state.tx.us/gis/sites.html. The cumulative outfall metric was based on cumulative amount of permitted discharge upstream of a site. Land-cover class percentages were calculated for each watershed using National Land Cover Database (NLCD 2001) available from http://www.mrlc.gov/nlcd_multizone_map.php. All GIS analysis was performed with ArcGIS 9.2 (ESRI, Redlands, CA.).

Table 4. Local-scale environmental variables (57) measured at Central Texas stream reaches.

Category	Abbreviation	Variable
Habitat type	HAB_TYPE	Habitat type score (riffle, run, pool, or glide) averaged across transects
	NO_RIFF	Number of riffles in study reach
Substrate	BEDROCK	Percent of substrate bedrock
	LG_BLDR	Percent of substrate large boulders (>45 cm)
	SM_BLDR	Percent of substrate small boulders (25-45 cm)
	COBBLE	Percent of substrate cobble (6-25 cm)
	GRAVEL	Percent of substrate gravel (2-60 mm)
	SAND	Percent of substrate sand (0.06-2 mm)
	MUDSILT	Percent of substrate mud or silt (<0.06 mm)
	GRV_LRG	Percent of substrate gravel or larger
	EMBEDDED	Substrate embeddedness (percent of boulders and cobble covered in fine sediment)
Algae/ macrophytes	ALGAE_AB	Abundance of algae in study reach (scored as abundant, common, rare, or absent)
	MCRPH_AB	Abundance of aquatic macrophytes in study reach (scored as abundant, common, rare, or absent)
Instream cover	STRM_COV	Visually estimated percent cover
	FILA_ALG	Percent of in-stream cover filamentous algae
	MICRALG	Percent of in-stream cover microalgae and biofilms
	MACRPHYT	Percent of in-stream cover aquatic macrophytes
	LWD	Percent of in-stream cover large woody debris
	SWD	Percent of in-stream cover small woody debris
	ROOTS	Percent of in-stream cover submerged roots
	OVR_VEG	Percent of in-stream cover overhanging vegetation
	UNDERCUT	Percent of in-stream cover undercut banks
	LEAFPACK	Percent of in-stream cover leaf packs
	BOULDER	Percent of in-stream cover boulders and other large substrates
	ARTIFICL	Percent of in-stream cover artificial objects
	COV_TYPE	Number of the above cover types present
Roots/woody debris	CWD_WET	Count of wetted coarse woody debris in study reach
	CWD_BKF	Count of dry coarse woody debris within bank-full stream width
	ROOT_WET	Count of wetted root wads in study reach
	ROOT_BKF	Count of dry root wads within bank-full stream width

Table 4. Continued.

Category	Abbreviation	Variable
Stream morphology	STRMBEND	Number of stream bends in study reach
	WELLBEND	Number well-defined stream bends in study reach
	MODBEND	Number moderately-defined stream bends in study reach
	POORBEND	Number poorly-defined stream bends in study reach
	WETWIDTH	Wetted width of stream (averaged across transects)
	AVG_DEP	Average stream depth
	THAL_DEP	Thalweg depth (averaged across transects)
	POOL_WID	Maximum pool width
	POOL_DEP	Maximum pool depth
	VELDEPTH	Velocity/depth regime score (optimal, suboptimal, marginal, or poor)
Flow	FLOWSTAT	Flow status score (high, moderate, low, or no flow)
	DISCHARG	Discharge (instantaneous stream flow in ft^3/s)
Riparian buffer	BUFFER	Width of riparian buffer (averaged across transects)
	RIP_TREE	Percent of riparian vegetation consisting of trees
	RIP_SHRB	Percent of riparian vegetation consisting of shrubs
	RIP_GRAS	Percent of riparian vegetation consisting of grasses/forbs
	RIP_CULT	Percent of riparian vegetation consisting of cultivated fields
	OTHER	Percent of riparian vegetation consisting of other types
	CANOPY	Percent of stream shaded by tree canopy (measured with densitometer)
Aesthetics	AESTHET	Aesthetics score (wilderness, natural area, common setting, or offensive)
Bank characteristics	BNK_SLOP	Bank slope (averaged across transects)
	EROSION	Percentage of bank with evident or potential erosion
	SOIL_EXP	Percentage of exposed soil on banks
Water parameters	DO	Instantaneous dissolved oxygen (mg/L)
	PH	pH
	SPCOND	Specific conductivity (μs)
	TEMP	Water temperature (°C)

Table 5. Landscape-scale environmental variables estimated for Central Texas streams. Land-cover percentages are for the watershed of a study stream.

Abbreviation	Variable
LAT_DS	Latitude, decimal degrees
LONG_DS	Longitude, decimal degrees
PRECIP	Mean annual precipitation, calculated for watershed
ELEV_M	Mean elevation (m)
WSLOPE	Mean watershed slope
WSHEDKM2	Watershed area (km^2)
DAMS_CT	Number of dams in watershed
OUT_MGD	Cumulative permitted outfall discharge rate within watershed (million gallons per day)
OUT_CT	Number of outfalls within watershed
RESV_CT	Number of reservoirs within watershed
RESV_PCT	% land covered in reservoirs
WATER	% land covered by water
DEV_TOT	% developed land
FOR_TOT	% forest land, including forested wetlands
SHRUB	% shrubland
GRASS	% grassland
PASTURE	% land converted for pasture
ROWCROP	% land converted for row crops
WET_TOT	% wetland
AG_TOT	% agriculture (row crop + pasture)
IMP_PCT	% impervious cover
CNPY_PCT	% canopy cover

I measured 29 functional traits (Table 6) of five adult individuals of each fish species collected in the study region. These traits were chosen because they have well known relationships with feeding, habitat use, swimming behavior, or life history strategies of stream fishes. For example, traits such as gape size, mouth position, head length and gut length relate to food resource use in fishes (Gatz 1979). Morphological features related to habitat preference and locomotion include relative body depth, fin dimensions, and dimensions of the caudal peduncle (Gatz, 1979, Webb 1984). Morphological traits were measured to the nearest 0.1 mm using vernier calipers following the methods of Winemiller (1991). For species with sexual dimorphism in

these traits (e.g., the anal fin of *Gambusia affinis*), only females were measured. Mean egg diameter, mean clutch size, age at maturation, and longevity were obtained from published studies and the FishTraits database (Frimpong and Angermeier 2009). These characteristics reflect interspecific differences in life history strategies (Winemiller & Rose 1992).

Table 6. List of the 29 functional traits used for Central Texas fish assemblages with measurement methodology. Trait definitions and functional categories follow Gatz 1979, Webb 1984, Winemiller 1991, Winemiller & Rose 1992, and Sibbing & Nagelkerke 2001.

Trait	Trait code	Trait definition	Category
Maximum standard length	MAX_SL	Maximum standard length from published records	Habitat use, feeding, life history
Head length	HEAD_L	Distance from the tip of the jaw to the posterior edge of the operculum	Feeding
Head depth	HEAD_D	Vertical distance from dorsum to ventrum passing through the pupil	Feeding
Oral gape	GAPE	Vertical distance measured inside of fully open mouth at tallest point	Feeding
Mouth position	MOUTH_P	The angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the center of the pupil and the posterior-most vertebra (e.g., 90° representing a terminal mouth)	Feeding, habitat use
Eye position	EYE_POS	Vertical distance from the center of the pupil to the ventrum	Habitat use
Eye diameter	EYE_D	Horizontal distance from eye margin to eye margin	Feeding
Snout length	SNT_L	Distance from the pupil to the tip of the upper jaw with mouth shut	Feeding
Snout protrusion	SNT_PR	Additional distance from the pupil to the tip of the upper jaw with mouth fully open and extended	Feeding
Body depth	BOD_D	Maximum vertical distance from dorsum to ventrum	Locomotion, habitat use
Body width	BOD_W	Maximum horizontal distance	Locomotion

Table 6. Continued.

Trait	Trait code	Trait definition	Category
Caudal peduncle length	PED_L	Distance from the posterior proximal margin of the anal fin to the caudal margin of the ultimate vertebra	Locomotion
Caudal peduncle depth	PED_D	Minimum vertical distance from dorsum to ventrum of caudal peduncle	Locomotion
Caudal peduncle width	PED_W	Horizontal width of the caudal peduncle at midlength	Locomotion
Body depth below midline	DEP_MID	Vertical distance from midline to ventrum	Locomotion, habitat use
Dorsal fin length	DORS_L	Distance from the anterior proximal margin to the posterior proximal margin of the dorsal fin	Locomotion
Dorsal fin height	DORS_HT	Maximum distance from the proximal to distal margin of the dorsal fin	Locomotion
Anal fin length	ANAL_L	Distance from anterior proximal margin to posterior proximal margin of the anal fin	Locomotion
Anal fin height	ANAL_HT	Maximum distance from proximal to distal margin of the anal fin	Locomotion
Caudal fin depth	CAUD_D	Maximum vertical distance across the fully spread caudal fin	Locomotion
Caudal fin length	CAUD_L	Maximum distance from proximal to distal margin of the caudal fin	Locomotion
Pectoral fin length	PEC_L	Maximum distance from proximal to distal margin of pectoral fin	Locomotion, habitat use
Pelvic fin length	PELV_L	Maximum distance from proximal to distal margin of pelvic fin	Locomotion, habitat use
Gut length	GUT_L	Length of gut from beginning of esophagus to the anus	Feeding
Gill raker length	RAKER_L	Length of the longest gill raker	Feeding
Egg diameter	EGG_D	Mean diameter of mature (fully yolked) oocytes	Life history
Clutch size	CLUTCH	Average clutch size	Life history
Longevity	LONGEV	Average life span in years	Life history
Age at maturation	AGE_MAT	Average age for reproductive maturity (in years)	Life history

Statistical analyses

I quantified among-site differences in taxonomic assemblage structure by performing non-metric multidimensional scaling (NMS) on log-transformed species abundances. Because it avoids assumptions of linearity, NMS is considered well suited for analyzing patterns in assemblage structure without some of the problems associated with other commonly used methods (McCune and Grace 2002). I used Bray-Curtis dissimilarity (BCD) as the distance measure, and retained a three-dimensional solution as stress values were substantially greater when only two axes were included in the ordination. A principal component analysis (PCA) was performed on log-transformed environmental variables (local and landscape-scale) to identify the primary environmental gradients among stream sites.

To examine among species differences in functional traits, a PCA was performed on the matrix of species traits. Because body size has a substantial influence on trait values, all traits were regressed against standard length and residuals were used as the trait values for the PCA. Mouth position and clutch size were not correlated with body size so log-transformed values for these variables were used instead of residuals. The PCA was performed using the mean transformed values for each functional trait for each species. The NMS and PCA analyses were carried out using PC-ORD software version 5.2 (MjM Software, Gleneden Beach, OR, U.S.A.).

An RLQ analysis was used to relate patterns of environmental differences and functional traits of fish assemblages among sites. RLQ is a multivariate technique based on ordinations of three separate matrices (species abundance, environmental variables, and species traits). RLQ was proposed by Doledec et al. (1996) to relate species traits directly to environmental characteristics through ordination of the matrix of species abundance for sites. The first step in RLQ analysis was the separate ordination of the species abundance, environmental variables, and species traits matrices. The “R” matrix containing the log-transformed environmental variables for the study sites was analyzed with PCA. The “L” matrix contains the log-transformed species abundances for sites, and correspondence analysis (CA) was used to identify gradients in taxonomic

assemblage structure following the RLQ specifications. Next, the functional traits of species in the "Q" matrix were analyzed using PCA on trait residuals. The significance of the relationship between the environmental variables and functional traits of species was tested with a Monte Carlo permutation test with 1000 random permutations of the rows of both the functional traits and environmental variables matrices (Doledec et al. 1996). The ADE-4 package (Dray and Dufour 2007) for R version 2.10.1 (The R Foundation for Statistical Computing) was used for all analyses associated with the RLQ.

Functional trait diversity was calculated for each fish assemblage using the convex hull volume method of Cornwell et al. (2006). The convex hull volume represents the multidimensional functional space filled by an assemblage, and it is calculated by measuring the volume within the minimum convex hull which includes the trait values for all of the species present. Because trait dimensions cannot be greater than the number of species when calculating the convex hull volume for local assemblages, we used the scores for the first six PC axes from the functional traits PCA for species' traits. These calculations were performed with the Quickhull algorithm (Barber et al. 1996) in MATLAB software (Mathworks Inc., 2009). Functional evenness, which describes the evenness of the distribution of species in functional trait space, was calculated following Villeger et al. (2008). Functional divergence, which describes how abundance is distributed in relation to the center of gravity of the functional trait space of a community, was calculated using the FDiv equation of Villeger et al. (2008). The FD package (Laliberte and Legendre 2010) for R version 2.10.1 (The R Foundation for Statistical Computing) was used to calculate functional evenness and divergence. Linear regressions were used to examine relationships between functional trait diversity of assemblages, species richness and primary environmental gradients. Trait volumes of assemblages were also regressed against IBI (Linam et al. 2002) and habitat quality index (HQI, Texas Commission on Environmental Quality 2007) scores calculated for the stream reaches (reported in Winemiller et al. 2009).

Results

A total of 60 fish species were collected over the study period, with richness per site ranging from 6 to 26 species with a mean of 14. Blacktail shiners (*Cyprinella venusta*), red shiners (*Cyprinella lutrensis*), western mosquitofish (*Gambusia affinis*), central stonerollers (*Campostoma anomalum*), and longear sunfish (*Lepomis megalotis*) constituted over 60% of the total sample. Most species were captured throughout the entire study region, but some were restricted to certain ecoregions and/or river basins. Nine species were collected at more than 40 sites, while 27 species were found at fewer than 10 sites. Common carp (*Cyprinus carpio*) was the only nonnative fish species collected in these streams.

The NMS analysis identified two axes that explained 85.4% of the variance in abundance of species among sites (stress = 16.68, instability = 0.003, 500 iterations) (Figure 14). Stream sites grouped together according to ecoregion in the NMS ordination, but they did not separate by river basin (Brazos or Trinity) on either axis. The primary axis (NMS 1, 54.2% variance explained) revealed a gradient which separates sites in the Cross Timbers ecoregion from sites in the East Central Texas Plains. This gradient tracks shifts in dominant substrate type and elevation that correspond with broad-scale physiographic differences between the regions. Fish species positively associated with axis 1 (more abundant in low-elevation sites with finer substrate) included *Lythrurus fumeus, Moxostoma poecilurum*, *Aphredoderus sayanus, Lepomis miniatus,* and *Etheostoma gracile*. Species including *Campostoma anomalum, Notropis volucellus, Moxostoma congestum, Etheostoma spectabile,* and *Percina macrolepida* were more abundant in the rocky, higher-elevation sites that plotted on the left side of axis 1. The second NMS axis (31.3% of variance) separated sites in the Texas Blackland Prairies ecoregion from sites in the other two ecoregions. This axis corresponds with a gradient of increasing urban and agricultural development in the watersheds of streams plotting near the top of axis 2. Local fish assemblages plotted at the top of axis 2 (greater urban and/or agricultural development) had lower species richness and contained more tolerant species such as *Cyprinella lutrensis, Pimephales*

vigilax, Gambusia affinis, Lepomis cyanellus, and *Lepisosteus* species. Many species were more abundant in the less developed sites at the bottom of NMS axis 2 including *Camposotoma anomalum, Cyprinella venusta, Lepomis microlophus, Etheostoma spectabile,* and *Percina sciera*.

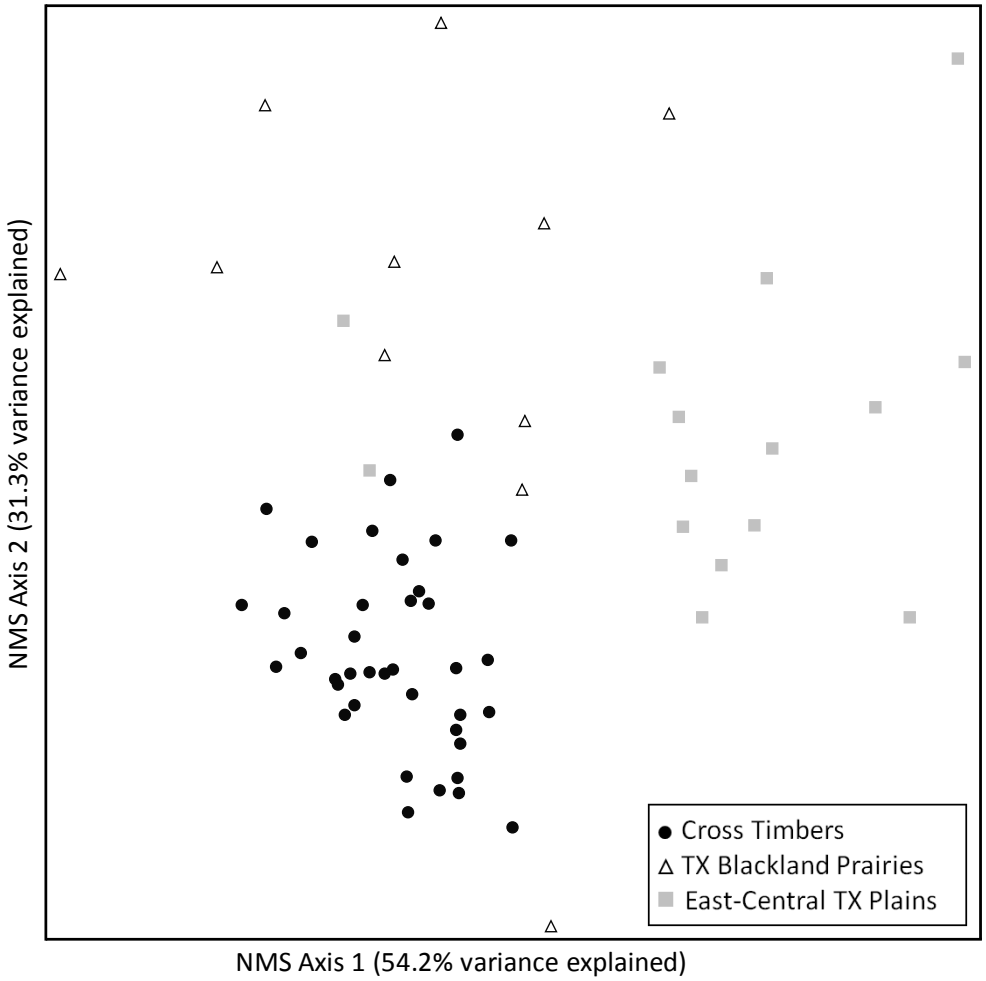

Figure 14. NMS ordination of Central Texas stream reaches based on species composition of local fish assemblages.

The 64 sites encompassed a variety of stream habitat conditions. Sites within the Cross Timbers ecoregion had greater stream widths, rockier substrates and more riffle habitats within study reaches. East-Central Plains streams generally had muddy or sandy substrates, more in-stream woody debris, and fewer riffles. Most stream reaches in the Blackland Prairies were in human-modified landscapes, had more homogeneous in-stream habitats, low canopy cover, and were intermediate between streams in the other two ecoregions in terms of substrate. The first two axes of the PCA on local and landscape-scale environmental variables explained 33.8% of total variation among stream sites (Figure 15). The dominant gradient (PC1, 23.5% of variance) was most strongly associated with substrate type, number of riffles, in-stream woody debris and roots, stream width, elevation, longitude, precipitation, percentage of grassland in the watershed, and percentage of land converted to pasture. Sites with high scores on axis 1 were generally within the East-Central Plains and had fine substrate, more roots and woody debris for in-stream cover, few riffles, and a greater percentage of pastureland in the surrounding landscape. Most stream reaches with low scores on axis 1 were in the Cross Timbers ecoregion and had rocky substrates, more riffles, wider channels, and more grassland in the watershed. The second gradient (PC2, 10.3% of variance) revealed a gradient that contrasted sites having more forest cover, more wetlands in the watershed and more in-stream cover with sites having less forest cover, more row-crop agriculture, extensive urban development, and more wastewater outfalls in the watershed. Sites with low scores on axis 2 were generally located in the northern portions of the Cross Timbers and the Blackland Prairies (near the Dallas and Fort Worth urban areas).

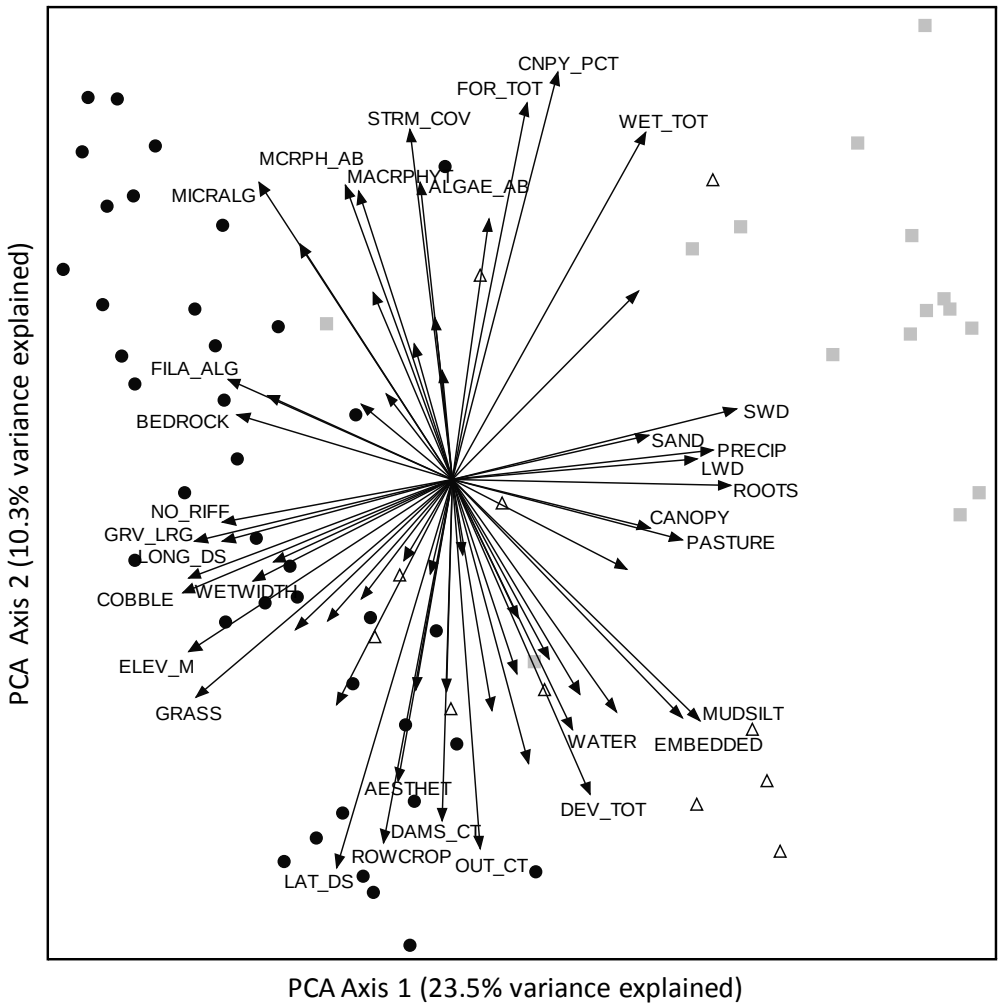

Figure 15. PCA ordination of Central Texas stream reaches based on local and landscape-scale environmental variables. Symbols represent the three ecoregions as in Figure 2. See Tables 4 and 5 for variable abbreviations.

Functional traits

PCA performed on functional traits resulted in two axes that explained 57.2% of variance among species (Figure 16). The primary axis (PC1, 44.8% of variance) largely reflected differences in head depth, body depth, fin lengths, gill raker length, eye diameter and eye position. Gar species (family Lepisosteidae), with very low body and head depths and relatively short fins had very high scores on axis 1. Centrarchid species have relatively deep bodies, long fins and large eyes, and they plotted on the negative end of axis 1. *Ictiobus bubalus*, *Carpiodes carpio*, and *Cyprinus carpio* also had very low scores on axis 1. Axis 2 (12.4% of variance) contrasted species with differences in trophic traits including head length, gape size, snout protrusion, gut length, and mouth position. More carnivorous species such as *Micropterus* species and *Lepomis gulosus*, with highly protrusible snouts, large gapes, and relatively short guts plotted at the top of axis 2. *Pylodictis olivaris* also had a high score on axis 2. Catostomid species (omnivorous benthic feeders) have subterminal mouths, long guts, and small gapes, and they had very low scores on axis 2. *Dorosoma cepedianum* and two herbivorous cyprinid species (*Hybognathus nuchalis* and *Campostoma anomalum*) also plotted at the bottom of axis 2.

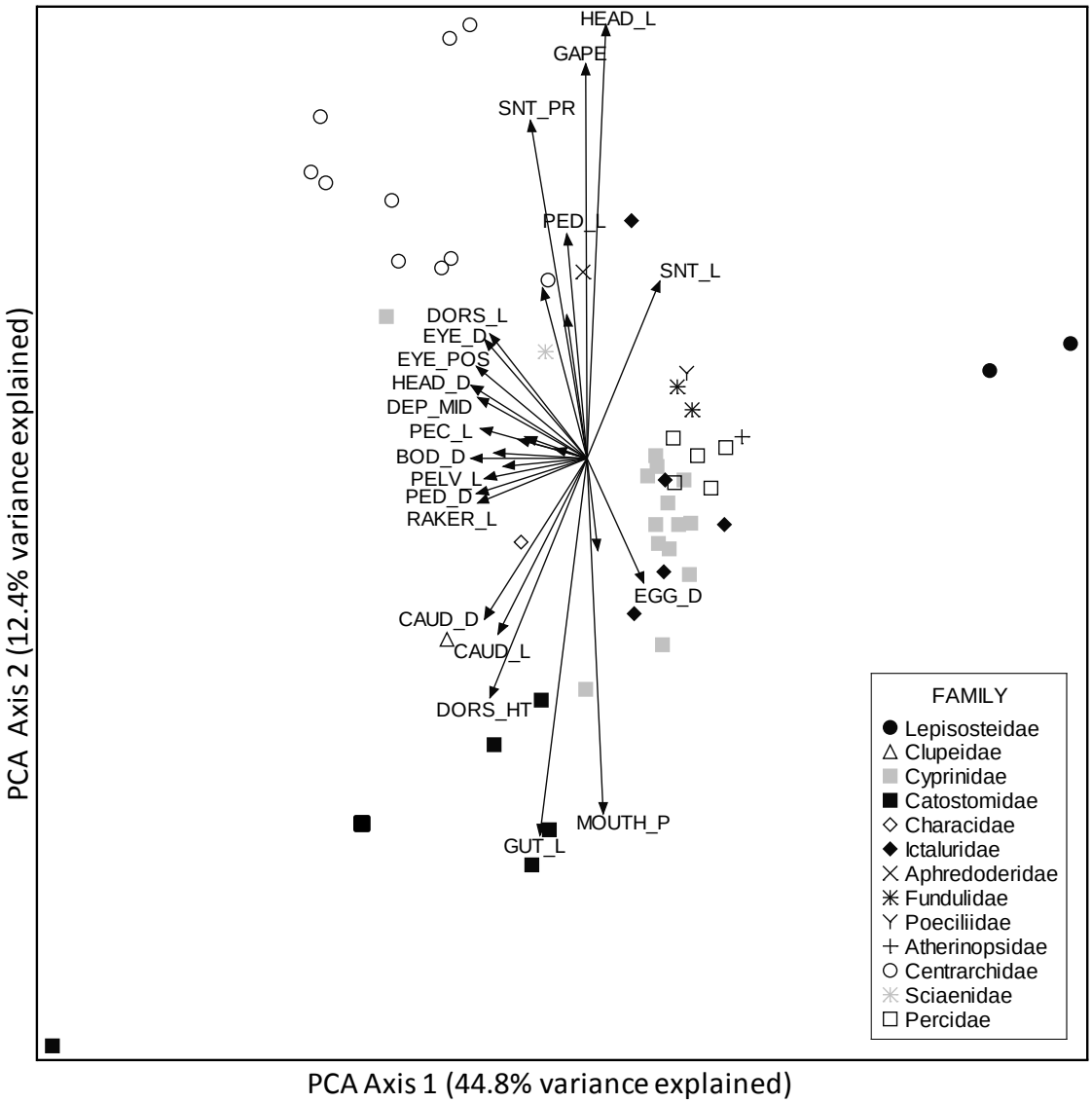

Figure 16. PCA ordination of Central Texas fish species in two dimensions of functional trait-space. Trait loadings on the two axes are depicted as vectors. Symbols represent the families of species. See Table 6 for trait abbreviations.

The RLQ analysis revealed a statistically significant ($P < 0.005$, 1000 permutations) association between the local and landscape-scale environmental variables and species traits. The first two axes of the RLQ accounted for 25.6% of the total

variance in the matrix that related the environmental characteristics of sites to the functional traits of species (Table 7). On RLQ axis 1, wider streams with grasslands in the surrounding landscape, wide riparian buffers, rocky substrate, and larger pool habitats plotted on the left side of the ordination contained species with larger body sizes, deeper bodies, longer fins, and larger clutch sizes (Figure 17). Plotted on the right side of axis 1, reaches with narrower channels, finer substrate, more in-stream woody debris, and more wetlands in the watershed generally contained smaller species with more streamlined body shapes, short gill rakers, and small clutches. Stream reaches within larger, more forested watersheds with higher discharge, more riffle habitats, and more diverse flow-depth regimes were positively associated with RLQ axis 2. Functional traits that correlated with RLQ axis 2 include inferior mouth position, body width, gut length and age at maturation. Environmental variables associated negatively with RLQ axis 2 include precipitation, amount of large woody debris, proportion of mud and silt in substrate, and the percentage of land in the watershed converted for pasture, row crops and urban development. Stream reaches plotted at the bottom of axis two contained species with superior mouths (such as *Gambusia affinis*), long heads and snouts, and long lifespan (such as *Lepisosteus* species).

Table 7. Results of the RLQ analyses for Central Texas stream fish assemblages. The ratios R/RLQ, L/RLQ, and Q/RLQ represent the percentage of variance in the separate analyses of the environmental variables (R), species composition (L), and functional traits (Q) accounted for by the first two RLQ axes.

	RLQ Axis 1	RLQ Axis 2
Eigenvalue	0.015	0.006
Covariance	0.122	0.077
Correlation	0.128	0.128
R/RLQ	75.6	78.2
L/RLQ	23.6	27.5
Q/RLQ	66.0	89.1

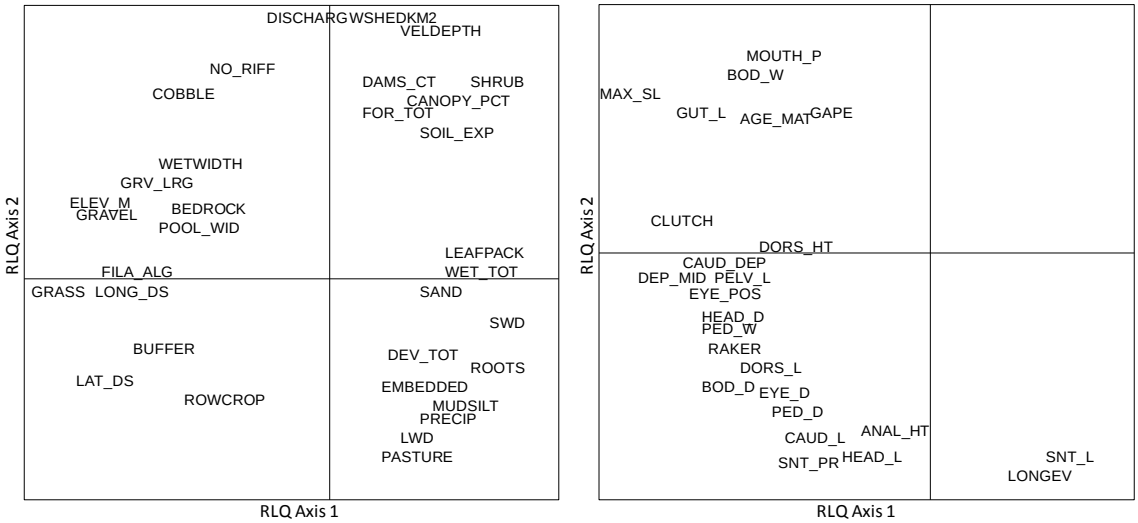

Figure 17. Ordination of RLQ scores of environmental variables and functional traits of fish species for Central Texas stream reaches. See Tables 4, 5, and 6 for environmental variables and functional traits that correspond to abbreviations.

The volume of functional trait space occupied by fish assemblages was significantly correlated with species richness of stream sites ($R^2 = 0.697$, $P < 0.0001$) (Figure 18). Sites with the largest functional convex hull volumes contained species from a broad range of families belonging to a variety of trophic guilds. Sites with higher IBI scores tended to occupy greater volumes of functional trait space ($R^2 = 0.347$, $P < 0.0001$). Some assemblages with intermediate species richness and IBI scores occupied the highest functional trait volume. These sites were characterized by species with distinctive morphology or life histories such as gars (*Lepisosteus* species), large sucker species (*Ictiobus*, *Carpiodes* or *Moxostoma* species), herbivorous minnows (*Campostoma anomalum* or *Hybognathus nuchalis*), shad (*Dorosoma cepedianum*), madtoms (*Noturus* species), flathead catfish (*Pylodictis olivaris)*, bass (*Micropterus* species), and darters (*Etheostoma* species). Functional trait space occupation also showed a weak but significant relationship with HQI score ($R^2 = 0.193$, $P = 0.0003$) and the first axis of the environmental PCA ($R^2 = 0.183$, $P = 0.0004$). Stream reaches with

higher HQI scores tended to occupy greater volumes of trait space, but there were many exceptions to this trend. Some sites that were rated highly in terms of habitat quality had relatively low species richness and functional trait diversity, while some of the most taxonomically and functionally diverse fish assemblages were in sites rated "intermediate" for habitat quality. Streams with high scores on axis 1 of the environmental PCA tended to have assemblages occupying a smaller volume of trait space, indicating that sites in the Cross Timbers ecoregion with rocky substrate, more riffle habitats, wider channels, and less development in the watershed (negative loadings on PC1) supported more functionally diverse assemblages. Some streams with high PC1 scores also contained assemblages occupying high volumes of trait space, however. Individual environmental variables significantly related to trait space occupation were percent of the watershed altered for agriculture (negatively correlated, $R^2 = 0.147$, $P = 0.002$), elevation (positively correlated, $R^2 = 0.135$, $P = 0.003$), and average channel width (positively correlated, $R^2 = 0.185$, $P = 0.0005$). Functional evenness and functional divergence showed no clear relationship with environmental variables or with IBI, HQI, or PC1scores.

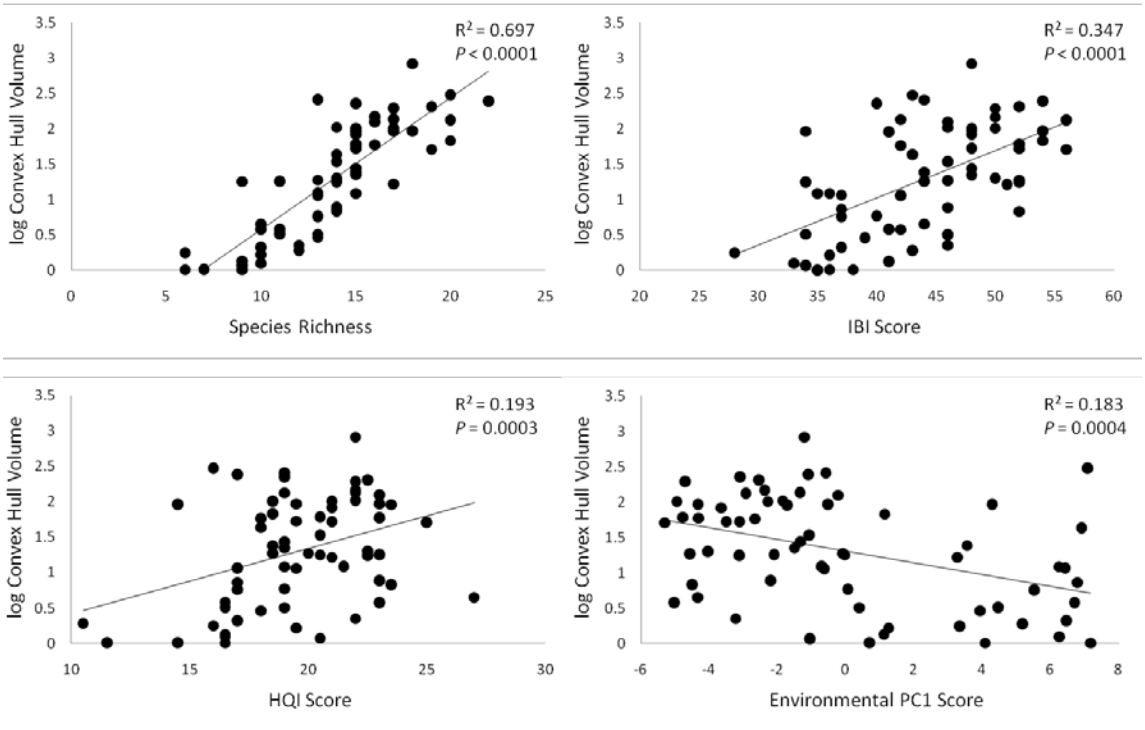

Figure 18. Regressions of convex hull volumes of functional trait occupation of Central Texas fish assemblages against species richness, IBI and HQI scores, and scores from the primary environmental axis (PC1).

Discussion

The taxonomic and functional structure of stream fish assemblages in this region were related to ecoregion-scale physiographic differences, landscape-scale gradients of urban and agricultural development, and local habitat variables. The dominant environmental gradient among stream sites (environmental PCA axis 1) separated sites according to elevation, precipitation, substrate type, presence of riffles, in-stream woody debris, and other characteristics correlated with broad-scale physiographic differences in climate, geology and terrestrial vegetation among the three ecoregions (Griffith et al. 2004). Along this gradient from the Cross Timbers to the Blackland Prairies and the East Central Plains, habitats generally changed from rockier streams with more riffles to streams with soft substrate and more woody debris. The ordination of stream reaches

based on taxonomic composition also revealed an influence of physiography on species distributions, with sites grouping together by ecoregion on the primary NMS axis. A second important environmental gradient among sites (environmental PCA axis 2) reflected differences in the degree of landscape alteration for agricultural and urban uses. This gradient contrasted sites with highly forested landscapes, extensive canopy cover, and more wetlands in the watershed with streams draining watersheds with more developed land and wastewater inputs. In terms of species traits, the main environmental variables related to functional structure of assemblages (highest correlations with RLQ axis 1 and 2) also included characteristics correlated with broad physiographic patterns such as elevation, substrate type, and amount of woody debris. Variables reflecting the extent of human land use in the watershed including amount of forest, total developed land, and percentage of land converted for row crops and pasture were also associated with functional trait composition.

Functional trait-environment relationships

The PCA based on species traits revealed that principal functional differences among species were associated with locomotion and habitat use (fin lengths, body depth, caudal peduncle dimensions) and trophic ecology (gut length, gape size, head length, snout length and protrusion, eye diameter, mouth position) and life-history strategy (egg diameter). Results of the RLQ analysis revealed the manner in which differences in the trait composition of local assemblages were related to environmental differences among stream sites. Large streams with more pool habitats contained larger species with deep bodies, long fins, and long gill rakers. This is in agreement with other studies that have found that body size of fishes is correlated with stream size (e.g., Schlosser 1982, Hoagstrom and Berry 2008) and that body shape is related to presence of pools in stream reaches (e.g., Lamouroux et al. 2002). Deep, laterally compressed bodies and long fins are traits known to improve maneuverability in low-velocity habitats with aquatic vegetation and other structures (Gatz 1979, Webb 1984). Gill raker length is associated with filter feeding in fishes (Gatz 1979), which is expected to be more common in

reaches with large pools based on the River Continuum Concept (Vannote et al. 1980) and findings of Poff and Allan (1995). In agreement with studies in other regions, smaller streams with narrow channels and few pools contained smaller species and species with more streamlined body shapes (Scarnecchia 1988, Lamouroux et al. 2002). Such traits are expected to be more common in smaller streams with fewer pools to provide refugia from high flows (Schlosser 1982, Townsend and Hildrew 1994).

Fishes with long intestines and subterminal mouths, such as catostomids and herbivorous cyprinids, were more abundant in wide stream reaches with rocky substrate and riffles within forested landscapes. Long intestines and subterminal mouths in fishes are associated with benthic omnivory (Gatz 1979, Hugueny and Pouilly 1999), and this trophic group has been found to be more abundant in larger streams with more vegetative detritus (e.g., Schlosser 1982, Goldstein and Meador 2004, Hoagstrom and Berry 2008). The amount of forested land cover in a watershed influences the quantity and type of detritus and in-stream cover in streams (Richards et al. 1996), and these factors likely enhance habitat quality for benthic omnivores. Streams with mud and silt substrates within more developed landscapes contained more small species with short reproductive cycles. These are considered resilience traits (Townsend and Hildrew 1994), and may provide an advantage in streams exposed to frequent disturbance (Winemiller and Rose 1992). Contrary to expectations, species with long lifespans were also relatively abundant in these reaches. This counter-intuitive result seems to be driven by the higher relative abundance of gars (*Lepisosteus* spp.), long-lived species considered relatively tolerant to human disturbance (Linam et al. 2002). Streams in developed landscapes also contained a higher proportion of species with superior mouth positions, such as *Gambusia affinis*. Such species forage near the surface of the water and can tolerate low-oxygen conditions more common in streams with greater landscape alteration and nutrient enrichment (Allan 2004).

As has been shown in studies comparing stream fish assemblages within regions (e.g., Hoagstrom and Berry 2008) and across continents (e.g., Winemiller 1991), functional trait-space occupation was greater in more species-rich assemblages. Volume

of trait-space was also highly correlated with IBI score, which is based on both taxonomic and functional attributes of assemblage structure (Linam et al. 2002). In general, the functional trait-space occupied by fish assemblages increased in streams with higher habitat quality scores located within landscapes with less alteration for agriculture and urban development. Conversion of natural landscapes for agricultural and urban development is considered an important cause of global decline in the integrity of lotic ecosystems (Allan 2004) and loss of aquatic biodiversity (Allan & Flecker 1993). Alteration of natural landscapes in watersheds has been shown to impact native fish communities directly and indirectly by altering local habitat characteristics (e.g., Wang et al. 2006, Rowe et al. 2009b). The influence of land use on the taxonomic structure of stream fish assemblages has been widely demonstrated (e.g., Roth et al. 1996, Walser and Bart 1999, Wang et al. 2001, Snyder et al. 2003), but the relationship between functional trait diversity and landscape alteration is poorly understood.

Implications for biomonitoring

Current indices of biotic integrity incorporate some functional aspects of fish assemblage structure (e.g., trophic guilds, pollution tolerance categories), but identifying specific functional traits or suites of traits related to stream habitat quality could potentially improve on these approaches and provide more sensitive and generally applicable metrics. These results show that in this region, functional trait composition of fish assemblages was related to local and landscape-scale variables that are influenced by anthropogenic disturbance. For example, traits related to locomotion and feeding ecology were related to the availability of pool and riffle habitats, reach-scale characteristics that are affected by flow regime alteration. Further study of these relationships could potentially be useful as water resource managers in Texas and elsewhere determine in-stream flow requirements for fishes. Also, trophic and life-history traits shifted in abundance along a land-use gradient, with larger species and herbivore/detritivores more common in streams within forested watersheds with less agricultural and urban development. This suggests that watershed landscape alteration

may have important functional consequences for fish assemblages and stream ecosystems in this region.

I suggest that such relationships likely translate across regions, and future research should aim to determine the predictability of assemblage-level functional responses to habitat degradation at larger geographic scales. Extensive research on functional traits along gradients of anthropogenic disturbance in stream invertebrate assemblages has yielded predictable relationships between land use and trait responses (e.g., Gayraud et al. 2003, Doledec et al. 2006, Tomanova et al. 2008). These results provide some insight into functional responses to anthropogenic disturbance by highlighting some potentially sensitive traits, but more research on how functional traits relate to landscape alteration, flow regime modifications, nutrient inputs, pollution, and climate change is necessary.

In summary, I found that local and landscape-scale environmental factors related to regional physiographic patterns and variables reflecting the extent of human land use influenced the functional structure of stream fish assemblages. Thus, the functional traits approach yielded patterns similar to those found in studies based on taxonomic assemblage structure, functional groups, or measures of taxonomic diversity. Functional descriptors of fish assemblage responses to environmental gradients provide a complement to traditional taxonomic measures (Angermeier and Winston 1999), and they offer an advantage in that they can potentially translate across basins, regions, and continents (Lamouroux et al. 2002). By continuing to document patterns of functional diversity and trait-environment relationships such as those shown here, we can gain a more mechanistic understanding of how environmental factors affect fish communities and improve our capacity to predict responses to environmental change (Poff 1997, Poff et al. 2006, Olden et al. 2010).

CHAPTER V

CONCLUSIONS

The structure of stream fish assemblages is potentially influenced by a multitude of factors, biotic and abiotic. In the research presented here, I focused on relationships between environmental variables at multiple scales and the functional structure of fish assemblages. An understanding of these relationships can potentially bolster our ability to predict how fish assemblages will respond to environmental change across geographic regions. My results suggest that environmental characteristics at the local, landscape and regional scales influenced the functional attributes of assemblages studied here. This implies that studies focusing only on local habitat variables may miss important influences on fish assemblage structure.

At the local reach scale, stream size, substrate characteristics, the availability of riffle and pool habitats, and abundance of in-stream cover structures were related to the functional trait composition of fish assemblages in the Río Grijalva Basin and in Central Texas streams. Landscape features most strongly related to functional structure in both regions were the extent of forested area in the watershed and the amount of land developed for urban and agricultural uses. At the regional scale, broad physiographic differences between ecoregions had a large influence on the taxonomic and functional composition of stream fish assemblages in Central Texas. Along the broad-scale longitudinal fluvial gradient of the Grijalva region, pronounced changes in the species composition, functional trait diversity, and trophic structure of fish assemblages were observed.

These results support the general framework presented by Poff (1997), which describes relationships between abiotic conditions and functional structure of stream assemblages as a series of environmental "filters." At the broadest scale, historical, biogeographic and climatic filters constrain the distribution of species, thus affecting assemblage structure. Results presented in Chapter III suggest that patterns in trophic structure along longitudinal fluvial gradients may vary due to large-scale differences

between temperate and tropical regions. At the regional scale, differences among ecoregions or among regions along a large river gradient constrained the functional structure of fish assemblages. For example, in the Grijalva basin, small, high-elevation headwater streams were dominated by fish species with more streamlined bodies (Chapter II). This was consistent with expectations based on the RHT (Townsend and Hildrew 1994), which predicts that fishes with more streamlined body shapes will be abundant in high-elevation streams because these forms are more resistant to fluctuating hydrology typical of headwater streams. At the landscape scale, results of the studies presented here suggest that the extent of development and loss of forest cover represents an important functional filter. Functional trait diversity in Central Texas and trophic diversity in the Río Grijalva basin were both lowest in streams within highly developed watersheds (Chapters III and IV). Several reach-scale factors appeared to influence the functional structure of stream fish assemblages in these two regions. For example, the presence of pool habitats was related to habitat-use and locomotion traits such as body depth and fin lengths in both regions (Chapters II and IV). Availability of riffle habitats was also related to functional structure, which suggests an important role for reach-scale filtering of traits by hydrological and geomorphological characteristics.

More research is needed to develop general relationships between functional structure of fish assemblages and environmental variables that can be applied across regions. Examination of trait-environment relationships in more regions is necessary to see if the functional structure of stream fish assemblages converges along similar environmental gradients despite taxonomic differences (Olden et al. 2010). Further study should aim to identify a subset of functional traits among the potentially large pool of traits that is most appropriate for predicting responses to environmental change.

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